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CYTOLOGICAL AND MORPHOLOGICAL STUDIES IN THE SOUTHERN AFRICAN IRIDACEAE

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ABSTRACT

This work is a cytological and morphological study of the southern African representatives of the Iridaceae. Hybridisation in the family is surveyed and several intergeneric crosses were attempted. A detailed examination of the chromosome cytology of several species in each genus was made. In all, 225 species in 43 genera were studied, 186 of these being new chromosome records, including 23 new reports for genera. The results were correlated with morphology and where applicable, with anatomy, and compared critically with the existing systematic treatments of the family. A new classification into tribes and subtribes is presented, and the circumscription of several genera is altered. As a result several changes in nomenclature were made, including a number of new combinations. The genus *Anomatheca* is upheld (previously a subgenus of *Lapeirousia*) while *Curtonus*, *Anaclanthe*, *Petamenes* and *Kentrosiphon* are reduced to synonymy. It is also suggested that *Acidanthera* be incorporated in *Gladiolus* but the necessary nomenclatural changes were not made.

UITTREKSEL

SITOLOGIE EN MORFOLOGIESE STUDIES IN DIE SUID-AFRIKAANSE IRIDACEAE.

Hierdie werk is 'n sitologiese en morfologiese studie van die Suid-Afrikaanse verteenwoordigers van die Iridaceae. Verbastering in die familie word ondersoek en 'n poging is aangewend om verskeie intergenetiese kruisings te doen. 'n Gedetailleerde ondersoek van die chromosoom sitologie van verskeie spesies in elke genus was gedoen. Daar was 225 spesies in 43 genera bestudeer, 186 van hierdie is nuwe chromosoom rekords en 23 nuwe verslae vir genera. Die resultate was met die morfologie gekorreleer en waar toepaslik, ook met anatomie, hulle was ook krities vergelyk met die bestaande sistematiese behandeling van die familie. 'n Nuwe klassifikasie in die stamme en substamme word voorgestel en die omskrywing van 'n paar genera is verander. Dus word verskeie naam veranderings gemaak sowel as 'n paar nuwe kombinasies. Die genus *Anomatheca* bly onveranderd (voorheen 'n subgenus van *Lapeirousia*) terwyl *Curtonus*, *Anaclanthe*, *Petamenes* en *Kentrosiphon* weer sinonime word. Dit word ook voorgestel om *Acidanthera* by *Gladiolus* in te lyf maar die noodsaaklike naam veranderings is nie gedoen nie.

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INTRODUCTION

The Iridaceae comprise a fairly large and homogeneous family of *Monocotyledonae*. It is agreed by most authors to be closely related to the *Liliaceae* and it is usually placed in the same order, *Liliales* although Hutchinson created a new order, *Iridales* for this family alone.

The distinguishing features of the family are its tricarpellary gynoecium with an inferior ovary, three stamens and equitant (isobilateral) leaves. There are exceptions to this last character in a few specialised genera, but here, the leaves are derived from the equitant type.

The classification of the family is in rather a confused state. Few authors agree as to the number or rank of the major groupings. Both the number of tribes (or sub-families) and the genera in them vary considerably and there is little agreement about which characters are significant in the classification of taxa above the specific level.

At present the family consists of about 65 genera and 1800 species. The size of the genera varies greatly as there are several monotypic groups, while others like *Iris* and *Gladiolus* contain more than 200 species. The distribution is worldwide but the region of greatest concentration is Africa, south of the equator. In southern Africa alone there are about 45 genera and 900 species recorded.

The figures quoted are necessarily rough estimates as few workers are agreed as to the number and limits of many genera and little general work has been done on the family for many years. Several genera urgently require revision and will probably be found to comprise fewer species than are at present recognised.

The present work is an attempt to elucidate some of the problems concerning classification and phylogeny and deals predominantly with South African taxa. The work involves a cytological investigation of the family, a new approach differing from the traditional use of only morphological characters for the classification of this group. It was hoped that certain morphological and cytological features could be linked so that the more significant characters for classification would be recognised. With the determination of these characters the rather vague and often arbitrary generic groups may then be recognised. In this way it is hoped that a better understanding of the family will be reached which may lead ultimately to the establishment of a natural classification.

Cytological studies of families and genera of plants have often proved extremely useful in solving problems of classification and taxonomy. The value of this aspect of investigation has been demonstrated amply by Levitsky in the Ranunculaceae, (fide Stebbins 1950), Babcock (1947) in *Crepis* and Simonet (1934) in *Iris*. In these studies confused or ambiguous situations, which could not be explained by extensive morphological investigation, were elucidated.

As cytotaxonomic studies deal mainly with chromosomal characteristics, it often happens that information on the phylogeny of generic groups is revealed and light is sometimes shed on methods of speciation, for example polyploidy and aneuploidy. The work of Raven and Kyhos (1965) on the evolution of the *Magnoliales* is an example of cytology indicating how evolution may have occurred. The use of chromosome studies in generic and specific taxonomy and in evolution is dealt with fully by Stebbins (1950), and in general his terminology and approach have been followed.

Little work has been done on the chromosome cytology of the Iridaceae. About one third of the genera have been examined, but quite randomly. Four genera only, *Crocus*, *Iris*, *Gladiolus* and *Romulea*, have been adequately investigated.

Owing to the numbers of species involved and the difficulty in obtaining live plants from other parts of the world, only the southern African genera are dealt with fully. As has been indicated, the majority of genera occur in this region and so it is hoped that a classification of these genera will prove significant for the classification of the family as a whole, or if not, at least show the line further investigation should take.

1. MATERIALS AND METHODS

A large number of species, representing as many genera as possible, was collected. Most often plants were collected in the field, though in some cases they were obtained from reliable horticultural sources. Wherever possible voucher specimens have been prepared, and unless otherwise stated, these were collected by the author and are housed at the Bolus Herbarium, Cape Town.

Lists of the species studied, together with the original localities and collector's number are given in tables in the chapters and sections dealing with the genera concerned (the abbreviations of herbaria are according to Index Herbariorum).

Chromosomes were studied mainly from mitosis in root tips and occasionally pollen mother cells were examined for meiotic phases. Although wild plants were almost invariably studied, it proved impractical to obtain root tips from plants in their natural state as the root system was usually found to be too extensive when they could be recognised in the field. The usual procedure was to collect plants in their native habitat and to let these dry off until the next growing season: spring in the summer rainfall area and autumn in the winter rainfall area. At this stage the corms were placed on damp sand in pots and the root tips harvested as they were produced. After sufficient root tips had been obtained, the corms were planted a few inches deep and grown to maturity when flowers could be obtained for further study if required. In the case of rhizomatous species, or when corms were not available, the root tips were obtained from germinating seeds or seedlings.

Root tips were harvested after midday on warm days as experience showed that this time was satisfactory, though not always optimum, for the observation of clear metaphase figures. The root tips were treated as follows:

Cytological Methods

Both wax section and squash methods were tried. In the former, root tips were fixed in Craf (Randolph 1935) and stored in 70% ethanol, or dehydrated immediately in a graded ethanol-n-butanol series, embedded in paraffin wax and sectioned 14—18 microns thick.

Two staining procedures were employed; either the aqueous Crystal Violet technique according to Smith (1934) or the Feulgen technique in which the method of preparation suggested by Kaston and Burton (1959) was used. Though initially the crystal violet stain gave good results, it was found to be unreliable and subsequently the Feulgen stain was used entirely.

When the squash method was used, root tips were pretreated in 0,05% colchicine for four hours and then fixed in acetic-ethanol, 1:3 for 10—15 minutes after which they were stored in 70% ethanol. After maceration in N-HCl at 60°C for about 8 minutes the meristematic portion of the root tips was placed in a drop of aceto-orcein (la Cour 1941) or lacto-propionic orcein (Dyer 1963) and squashed under a coverslip.

Preparations of pollen mother cells were obtained by squashing fresh anthers directly on to slides and staining in aceto-orcein or lacto-propionic orcein.

After experimenting with the various methods, it was decided that the paraffin wax section method would be followed. This was because although the squash method gave good results it was not suitable for species with small chromosomes as these could only be seen with difficulty. The wax section method also had the advantage of yielding permanent preparations which could be viewed at leisure and referred to subsequently. Permanent mounts with the squash method could only be obtained with difficulty and were frequently not satisfactory, although using the lacto-propionic orcein of Dyer, material did last for a few weeks. Squash preparations were, however, frequently made for plants with very large chromosomes as these could often be studied more easily than in sections, particularly if the chromosome number was high.

Drawing Technique and Representation of Karyotypes:

All cytological drawings were made with the aid of a camera lucida and a 25 × ocular. Although many metaphase plates were drawn for each species, only a single illustration is shown in this work. All the chromosomes illustrated were drawn from wax section preparations and are thus directly comparable.

Where chromosomes details were distinct, and homologous chromosomes could be recognised, the karyotype has been represented diagrammatically by means of an idiogram. This represents the haploid complement of chromosomes and greatly facilitates comparision of different karyotypes. The idiograms are compiled from at least three good metaphase plates and as there is always some variation in observed chromosome size owing to the degree of condensation, the idiogram may not exactly match the particular metaphase illustrated.

2. CLASSIFICATION SYSTEMS OF THE IRIDACEAE

The four important basic systems of classification of the Iridaceae are those proposed by Bentham & Hooker (1883), Pax (1888), Hutchinson (1934) and Lewis (1954). Earlier systems such as that of Klatt (1882) were based on too little information and are not of any importance today.

1. The classification of Bentham & Hooker.

In this very early classification of the family, it was divided into three tribes: *Moraeeae*, *Sisyrinchieae* and *Ixieae*. The tribes were defined as follows:—

Moraeeae:	inflorescence a cymose corymb; flowers fugitive; stamens opposite the style branches.
Sisyrincheae:	inflorescence a cymose corymb; flowers fugitive; stamens alternate to style branches.
Ixieae:	inflorescence a spike; flowers not fugitive.

The only tribe which Bentham & Hooker subdivided was the *Sisyrinchieae* where they created four subtribes, defined as follows:

Croceae:	rootstock a tunicate corm; spathes single flowered; scape single flowered.
Cipureae:	rootstock a tunicate corm; spathes 2-flowered perianth tube short or absent; perianth segments subequal.
Eusisyrinchieae:	rootstock a rhizome; spathes 2-flowered; perianth tube short or absent; perianth segments equal or subequal in most or inner segments smaller.
Aristeae:	rootstock a short or creeping rhizome, or roots arising from a woody stem; perianth tube developed to some extent; capsule often included in the spathes.

The system was followed by Baker in Flora Capensis (1896) and also by Diels (1930) in the second edition of Engler & Prantl's *Pflanzenfamilien*, although he altered the sequence to place the *Moraeeae* at the end instead of the beginning. This system also formed the basis of Hutchinson's system.

2. The classification of Pax.

This classification, produced in 1888, appeared in the first edition of the *Pflanzenfamilien* of Engler & Prantl. Here the family is divided into three sub-families: the *Crocoideae* (Bentham & Hooker's subtribe of the *Sisyrinchieae*), the *Iridoideae* corresponding to the *Moraeeae* and the remainder of the *Sisyrinchieae*, and the *Ixioideae* corresponding to the *Ixieae* of Bentham & Hooker. These sub-families were defined as follows:

Crocoideae:	reduced plants with solitary flowers lacking an aerial stem.
Iridoideae:	inflorescence a many flowered cyme enclosed in spathes borne on an aerial stem.
Ixioideae:	inflorescence a spike composed of many solitary flowers enclosed in spathes.

Here great stress is placed on the inflorescence. This is unsatisfactory as there are many different interpretations of the Iridaceous inflorescence and there are several exceptions at both specific and even generic levels in each sub-family. Pax subdivided his *Iridoideae* and *Ixioideae* into several tribes. In the *Iridoideae* he recognised four tribes, two out of Bentham & Hooker's *Moraeeae* and two out of their *Sisyrinchieae*. Pax changed the position of one group, the *Cipureae* as he removed it from amongst the *Sisyrinchieae* (of Bentham & Hooker) to a position in the tribe *Tigrideae* among genera which Bentham & Hooker regarded as belonging in their *Moraeeae*.

In Pax's system the *Ixieae* are for the first time divided into tribes. His basis for division was the nature of the flower and style branches. The tribes and their characteristics are as follows:—

Ixieae: flower actinomorphic; style branches undivided.
Gladioleae: flower zygomorphic; style branches undivided.
Watsonieae: flower zygomorphic; style branches divided.

This system was followed by Rendle (1904) and by Marloth (1915) in his Flora of South Africa. It has been superseded by that of Diels (1930) who reverted to the Bentham & Hooker system.

3. The classification of Hutchinson.

Hutchinson proposed a third classification of the Iridaceae in his *Families of Flowering Plants* (1934). He placed the Iridaceae alone in the order *Iridales* and within the family recognised eleven tribes of equal rank. The system is essentially that of Bentham & Hooker, though their tribes are divided and the genera arranged slightly differently. The *Moraeeae* are divided into three, the *Sisyrinchieae* into four (including the *Crocoideae* of Pax as one) the *Ixieae* into three, and one new one is created consisting of a primitive genus *Hewardia* or *Isophysis*, the presumed Iridaceous ancestor which has six stamens. In making his groups all of equal rank, the natural relationship between some of the tribes is obscured and this makes the system seem artificial and difficult to follow.

For his classification Hutchinson used quite different criteria from previous workers. The type of rootstock is considered important, especially for recognition of genera, but greatest significance is given to the flower and its progressive zygomorphy. This classification appears to be rather different from the previous two, but is actually similar except that the rank of several groups is changed.

The system of Bentham & Hooker and correspondingly of Hutchinson, was modified by Weimarck (1940). He considered that as the *Sisyrinchieae* are characterised by the lack of a perianth tube and the *Aristeae* by having one, *Aristea* itself was misplaced for it lacks a perianth tube. Thus he placed this genus in the *Sisyrinchieae* and the remaining genera of the *Aristeae* in the *Niveniinieae*, a new tribe, thus abolishing the tribe (or subtribe) *Aristeae*.

4. The classification of Lewis.

Lewis (1954) proposed a fourth classification of the family. She dealt only with South African species and recognised three tribes distinguished as follows:—

Irideae: inflorescence not spicate; flowers fugaceous, pedicellate and arranged in cymes.
Nivenieae: as above, but flowers not fugaceous; plants shrubby and exhibiting secondary growth.
Ixieae: inflorescence usually a spike; flowers not fugaceous, sessile with perianth tube.

This classification is most similar to that of Pax although the highest rank is the tribe, not subfamily. Lewis placed the woody genera in a tribe apart from *Aristea* with which they are usually grouped, for she considered their shrubby habit and secondary growth as very distinct features. Following Pax, the rather primitive *Aristea* is placed in the same tribe as *Moraea* and its allies, though in different subtribes. Lewis disregarded Pax' major group, the *Crocoideae* and she shows conclusively that it was an artificial unit comprising genera belonging to the *Irideae* and *Ixieae*.

3. HYBRIDISATION

Other than in the genera *Iris*, *Crocus* and *Gladiolus*, comparatively little critical work has been done on hybridisation in the Iridaceae. In other attractive cultivated genera many species have been hybridised to some extent by horticulturists.

There is a large number of hybrids in *Iris* and *Crocus*. Among these are some carefully produced experimental hybrids and here meiosis has been studied (Simonet 1934). Studies of hybrids in *Iris* have been of great value in suggesting the origin of some species (Randolph and Mitra 1959) and have also indicated the interrelationships and possible evolution of the different sections of *Iris* (Simonet 1934).

No comparable work has been done on any of the other genera except *Gladiolus*, where hundreds of crosses have been made in the search for new, horticulturally valuable forms. This work has been reviewed by Bamford (1935; 1941) and has recently been discussed by Hamilton (1968). It is known that several levels of polyploidy occur in *Gladiolus* and Bamford's work has shown that the diploid species are interfertile and produce fertile offspring. The diploid species can also be crossed with polyploids; the offspring in these crosses are not fully fertile but can be back crossed to some extent to the diploids. Most of the commercial varieties of *Gladiolus* are high polyploids and are the result of interbreeding between several different species. Intergeneric crosses among *Gladiolus* and *Homoglossum* or *Acidanthera* have also been reported and this will be discussed fully in the section on *Gladiolus* and its allies.

In other genera which are frequently grown in gardens most crossing appears to have been quite random and even accidental. In this manner numerous hybrids of *Tritonia*, *Sparaxis*, *Watsonia*, *Ixia*, *Babiana* and *Freesia* have come into existence and many of these have been named or even described as distinct species (Brown 1935; Goldblatt 1969). Because of its horticultural value, *Freesia* has received much attention from plant breeders. Attempts have been made to find wild species with which to increase variation in the cultivated forms; these are derived from only a few species according to Brown (1935). The varieties of *Freesia* cultivars are the product of considerable selection and today almost all garden *Freesias* are polyploid. Many of the hybrids of *Ixia* now in cultivation are also polyploid (Brittingham, 1934) and it is likely that many forms in other cultivated genera are polyploid.

As hybrids are so easily obtained and many of the cultivated forms are polyploid, it is clear that cytological studies in the family must be done only on specimens collected in the wild. Those obtained from commercial sources will always be suspect and indeed are a likely source of many of the anomalous chromosome counts reported from time to time.

The studies in *Romulea* by de Vos (1965) have added to the information on hybrids in the Iridaceae. She reports that a few natural hybrids between closely related species occur. However, under artificial conditions many more hybrids can be obtained. Her results show that in general, related species with similar or the same chromosome numbers will hybridise and produce viable offspring, but in some cases the crossing of related species and varieties unexpectedly fails and it must be presumed that there is a reproductive barrier between these forms. The more distantly related species cross less easily, or not at all, which is not surprising in a genus where such a great range of chromosome numbers occur.

In a valuable study of hybridisation in *Watsonia*, *Ixia* and *Sparaxis*, Horn (1962) showed that most species in each genus are interfertile and yield fully fertile offspring. He found that species in these genera are normally cross-pollinated and that species were self-compatible, but when selfed, produced very few seeds. This observation can be confirmed by the present author for *Ixia* and *Sparaxis*. It is clear, however, that this phenomenon is not universal in the Iridaceae, for all *Gladiolus* species grown by the author are self-sterile and do not set seed unless cross-pollinated.

The ease with which Horn produced interspecific hybrids explains why so many garden hybrids occur. Hybrids are rare in nature although they have been reported in *Watsonia* and *Babiana* by Lewis (1950; 1959). Several putative hybrids exist in herbaria but these are by no means proven. The fact that natural hybrids are so uncommon suggests that external isolating factors operate to prevent interspecific hybridisation taking place.

As it is clear that there is little difficulty in obtaining interspecific hybrids and that these would in any case contribute little to the existing knowledge of interrelationships in the family, the author has in most cases attempted to produce intergeneric hybrids. It was presumed that any successful crosses would indicate close generic relationships or at least indicate certain affinities. Not surprisingly, few of these crosses proved successful but several interesting results were obtained. (Table 1).

Crosses were only attempted where some measure of success could be expected. Thus genera were crossed when it was known or suspected that these were related or had a similar karyotype. Crosses were made in the normal way by emasculation before anthesis, bagging and transferring pollen to the isolated stigmas when these were receptive. Wherever possible reciprocal crosses were made.

The significance of the results of each cross will be discussed in the relevant section on each group of genera.

TABLE 1

List of interspecific and intergeneric crosses made by the author. The results of each cross and condition of any offspring are indicated.

Crossing	Normal Seed in Fruit	Hybrids
Dierama pendulum × Ixia conferta	0	—
Ixia conferta × Dierama pendulum	0	—
Hesperantha vaginata × Geissorhiza leipoldtii aff. .	0	—
Geissorhiza leipoldtii aff. × Hesperantha vaginata .	2	No germination
Moraea ramosissima × Dietes bicolor	0	—
Dietes bicolor × Moraea ramosissima	0	—
Dietes vegeta × D. bicolor	0	—
Dietes bicolor × D. vegeta	0	—
Homeria elegans × Homeria miniata	Many	Healthy not yet flowered
Freesia muirii × Anomatheca viridis (Lapeirousia) .	0	—
Anomatheca viridis (Lapeirousia) × Freesia muirii .	0	—
Anomatheca juncea (Lapeirousia) × Freesia refracta .	0	—
Geissorhiza heterostyla × Gladiolus fasciculatus .	0	—
Gladiolus fasciculatus × Geissorhiza heterostyla .	0	—
Schizostylis coccinea × Hesperantha falcata . . .	Several	No germination
Dierama pendulum × Sparaxis elegans	0	—
Sparaxis elegans × Dierama pendulum	0	—
Gladiolus fasciculatus × Anomalesia cunonia . .	Many	Healthy not yet flowered
Anomalesia cunonia × Anomalesia saccatus (Kentrosiphon)	Many	Viable seed
Gladiolus cardinalis × Gladiolus buckerveldii (Petamenes)	Many	Healthy seedlings
Gladiolus buckerveldii (Petamenes) × Gladiolus cardinalis	0	—

4. DISCUSSION

The cytology, cytotaxonomy and possible phylogeny of the genera.

The cytological or strictly speaking karyological observations can be discussed at two levels. Firstly, at the family level where it can be seen that the genera of the Iridaceae fall into natural groups based on general chromosome morphology and secondly, at the generic level where in most cases, genera or small groups of genera, have similar karyotypes. Morphological and karyological features can frequently be linked so that the most significant characters for classification can be recognised. In this way generic relationships are often indicated, and subtribes can be distinguished. Phylogenetic trends are sometimes indicated and the evolution of some groups is suggested.

Two tables are provided to facilitate comparisons of cytological data in the different genera and tribes (Table 2, 3). The diploid and suggested basic number are listed for each genus and the chromosomes have been divided arbitrarily into size categories to show similarities and differences in length.

4.1 THE CLASSIFICATION AT SUBFAMILY LEVEL AS SUGGESTED BY THE CYTOLOGY

It can be seen from cytological observations that there are two recognisable series of karyotypes. One group has relatively large chromosomes, which under the treatment described, range from 4 to 10μ, though sometimes smaller, and the other group has small chromosomes ranging from 1 to 5μ. This appears to be significant as there is a strong correlation between these karyotypic groups and the major subdivisions of the family proposed by various authors.

All the genera of the tribe *Moraeeae* (sensu Bentham & Hooker) belong to the group with long chromosomes. Of the fifteen genera in this tribe, twelve have been cytologically examined, at least to a small extent and all have large chromosomes.

Short chromosomes are found in all the genera of the Ixieae (sensu Bentham & Hooker) that have been examined. Since Bentham & Hooker, the concept of this tribe has altered only a little in that some members of the *Crocoideae* were placed here by Lewis. At present the number of genera in the tribe is 36 and all but four have been cytologically studied. Although cytological evidence does partly support Lewis in placing the *Crocoideae* in this tribe, *Crocus*, one of the genera involved, proves to be the exception in the tribe in having many species with long chromosomes. This appears to be anomalous and suggests that *Crocus* is perhaps misplaced in the classification. There is, however, some evidence that the large chromosomes may be a specialised condition in *Crocus* and this will be discussed fully under the section on *Romulea* and its allies.

The *Sisyrinchieae* of Bentham & Hooker is an unnatural group and even as modified by Lewis, who removed the *Crocoideae* from here, it remains rather heterogeneous. There are about 20 genera in this group and unfortunately only eight have been cytologically investigated. The chromosomes are small and in those species studied by the present author, are as small as the smallest chromosomes in the *Ixieae*. One exception is *Bobartia*, placed in the subtribe *Sisyrinchiineae* (previously *Eusisyrinchieae*). It has rather large chromosomes and its present position requires further elucidation.

The *Sisyrinchieae* have been altered in concept by Weimarck and further by Lewis who removed the *Crocoideae* to the *Ixieae*. In its modified composition it contains genera which are the least specialised in the family. The rootstock is a rhizome, the leaves are unmodified and the inflorescences usually much branched with regular flowers which only rarely have a perianth tube. Cheadle

(1964) who investigated the xylem elements in the family, found that *Aristea* and its allies were in this respect by far the least specialised. Thus a large part of this group can be regarded as primitive and it should be placed at the beginning of the classification.

There has not been sufficient cytological study of the *Sisyrinchieae* to enable the cytological data to be used to evaluate its taxonomic circumscription. Most of the few genera examined have small chromosomes and are clearly distinct from the *Moraeeae* so that the treatment of Pax, who merged the *Sisyrinchieae* and *Moraeeae* together in a single subfamily, cannot be supported. At the present state of our knowledge, the *Sisyrinchieae* should be maintained as a single tribe, though perhaps it may be found to consist of two or more groups of equal rank with the *Moraeeae* and *Ixieae*, as did Hutchinson.

Table 2

The karyotypic features of genera in the tribes *Sisyrinchieae* and *Irideae* studied by the present author. Somatic number, a suggested basic number and the relative length of the chromosomes are shown.

Genus	Somatic No. 2n	Suggested Basic No. x	Description		
			Long = $>4\mu$	Med.	Short = $<2{,}5\mu$
Tribe SISYRINCHIEAE					
Aristea	32, 64	16	—	—	16
Klattia	32	16	—	—	16
Nivenia	32	16	—	—	16
Patersonia	24	12	—	1	11
Witsenia	32	16	—	—	16
Bobartia	20	10	4	6	—
Tribe IRIDEAE					
Dietes	20, 40	10	7	3	—
Ferraria	20, 60	10	5	5	—
Moraea	20, 24, 18, 12	10	7	3	—
Gynandriris	12	6	6	—	—
Galaxia	16, 32	8	5	3	—
Homeria	12, 24, 36	6	6	—	—
Hexaglottis	12, 10	6	6	—	—

The genera which require study for the understanding of *Sisyrinchieae* are mainly South American, but a few are Australasian. Until these are satisfactorily examined, none of the existing subdivisions of this tribe can be validated.

The *Moraeeae* appear to be a natural group and should be maintained as the second major group in the family. According to the code of botanical nomenclature the name of a taxon below family rank must be derived from the same stem as the next higher taxon when it contains the type of this taxon. Consequently, *Moraeeae* is illegitimate and the name *Irideae* as substituted by Lewis must be followed. As this group is somewhat specialised it should not be placed at the beginning of the classification but rather after the *Sisyrinchieae*.

TABLE 3

The karyotypic features of genera of the tribe *Ixieae*. Somatic number, a suggested basic number and relative length of the chromosomes are shown.

Genus	Somatic No. 2n	Suggested Basic No. x	Description		
			Long = $>4\mu$	Med.	Short $<2,5\mu$
Tribe IXIEAE					
Pillansia	44	11	—	—	11
Thereianthus	20	10	—	1	9
Micranthus	20	10	—	1	9
Watsonia	18, 27	9	—	2	7
Tritoniopsis	32	16	—	—	16
Anapalina	34	17	—	—	17
Lapeirousia	20, ?18	10	1	—	9
Anomatheca	22	11	—	1	10
Freesia	22	11	—	1	10
Schizostylis	26	13	—	—	13
Hesperantha	26	13	—	—	13
Geissorhiza	26, 39, 52	13	—	—	13
Engysiphon	26	13	—	—	13
Melasphaerula	22	11	—	—	11
Gladiolus	30, 45, 60	15	—	—	15
Acidanthera	30	15	—	—	15
Radinosiphon	30	15	—	—	15
Homoglossum (including Petamenes)	30	15	—	—	15
Anomalesia	30	15	—	—	15
Romulea	32–18, 44, 54	12	—	—	12
Syringodea	12, 22	6	—	2	4
Dierama	20	10	—	2	8
Ixia	20, 40	10	—	2	8
Sparaxis	20	10	—	2	8
Synnotia	20	10	—	2	8
Tritonia	22, 44	11	—	2	9
Crocosmia (including Curtonus)	22	11	—	2	9
Chasmanthe	20	10	—	2	8
Antholyza (including Anaclanthe)	14	7	2	1	4
Babiana	14	7	2	1	4

Hutchinson's treatment which divides the *Irideae* into three tribes is not convenient as the relationship among the genera in these tribes is then obscured. In this respect the Bentham & Hooker system is better, although the genera within this single unit could perhaps be grouped naturally into subtribes following Hutchinson's subdivisions. The inclusion by Pax of the *Cipureae* of Bentham & Hooker in this group cannot be commented upon, for none of the genera have been cytologically investigated.

The *Ixieae* are also a natural group both morphologically and cytologically and except for Hutchinson, who divided the group into three equal ranking tribes, has been regarded as a single entity. Hutchinson's treatment is artificial for it results in the placing of related genera with similar karyotypes in different tribes. Clearly the *Ixieae* must remain as one of the major groupings within the family. Bentham & Hooker's treatment must, however, be modified to include the *Croceae* as Lewis proposed. The genera of the *Ixieae* have, with one exception, a cormous rootstock, the inflorescence is usually a spike and in several genera extremely zygomorphic flowers are found. On these grounds the tribe is considered to contain the most specialised plants in the family and should be placed last in the classification, as was done by Bentham & Hooker.

4.2 Tribe 1. *SISYRINCHIEAE.*

The *Sisyrinchieae* comprises plants with the least specialised rootstocks in the family, these being either unmodified or rhizomatous. The leaves are of the equitant type, the flowers are arranged in cymose clusters and are generally fugaceous and actinomorphic. The stamens are alternate to the style branches or lobes.

Cytotaxonomy and possible phylogeny.

Subtribe 1. ***Aristeineae.***

Aristea, *Patersonia*, *Nivenia*, *Witsenia* and *Klattia*.

This group consists of relatively unspecialised plants with an unmodified rootstock or a rhizome. The South African representatives of the group, as well as the Australian genus, *Patersonia*, are dealt with. The group comprises both herbaceous and woody or shrubby plants, the latter being *Nivenia*, *Witsenia* and *Klattia*. The flowers are unspecialised, actinomorphic and the style is undivided.

ARISTEA

$2n = 32, 64.$

This genus comprising about fifty species is distributed widely over sub-Saharan Africa and in Madagascar, occurring in montane regions in the tropics, but in the lowlands as well in the temperate south, where the largest number of species is found. The plants are typically herbaceous, blue flowered and lack a perianth tube.

Twelve of the approximately fifty species were examined cytologically. (Table 4). In all but two species the diploid number of 32 was obtained. One population of *A. glauca* and the South African form of *A. ecklonii* were found to be polyploid, having a somatic number of 64. In all cases the chromosomes are very small and often difficult to examine. Little size difference is noticeable, all chromosomes being from 1 to 5μ long. Most of the chromosomes are acrocentric though occasionally sub-metacentric ones can be distinguished. Satellites were seen only rarely but in *A. bicolor* two were observed. No idiogram has been compiled owing to the great similarity of the chromosomes. (fig. 1).

There have been only two previous chromosome counts in this genus (Table 4). Fernandes & Neves (1961) found a somatic number of approximately 65 in *A. ecklonii* while Riley (1962) reported a diploid number of 32 in *A. major*. In the present work the count for *A. major* is confirmed and somatic numbers of 32 and 64 were found in different populations of *A. ecklonii*. It appears that the plant studied by Fernandes & Neves was a polyploid and probably had 64 chromosomes.

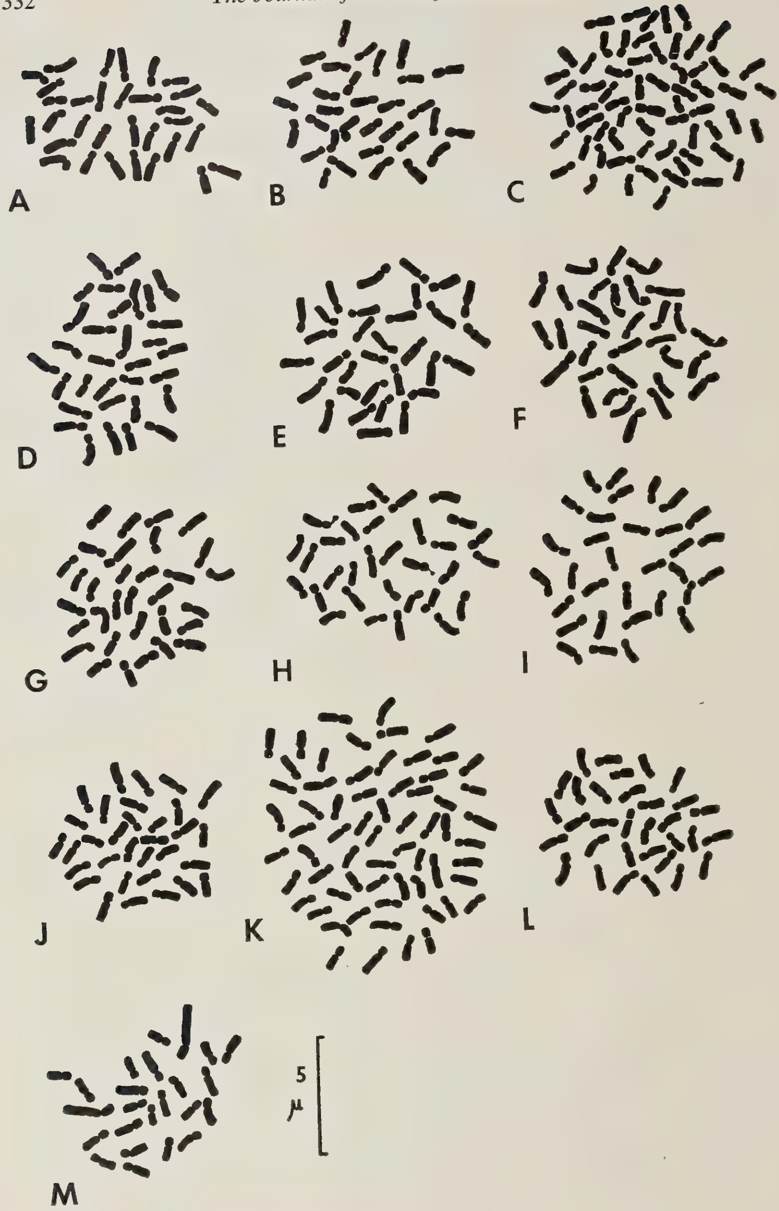
TABLE 4

Chromosome numbers in *Aristea, Patersonia, Nivenia, Witsenia, Klattia* and *Bobartia*.

Species	Diploid No.	Collection Data or Reference
ARISTEA Ait.		
A. woodii N. E. Br.	32	Sabie, Tvl. *Goldblatt 81* (*J*)
A. ecklonii Bak.	64	Haenertsburg, Tvl. *Goldblatt 3* (*J*)
	±65	(Fernandes & Neves 1961)
A. ecklonii Bak. var.	32	Chimanimani Mountains, Rhodesia *Goldblatt 151, 164* (*J*)
A. confusa Goldblatt (=capitata)	32	Kalk Bay, C.P. *Goldblatt 416*
A. major Andr. (=thyrsiflora)	32	Constantia, C.P. *Goldblatt 399*
(as thyrsiflora)	32	(Riley 1962)
A. spiralis (L.f.) Ker.	32	Klein River Mnts., C.P. *Goldblatt 418*
A. monticola Goldblatt (=A. coerulea)	32	Ceres, C.P. *Goldblatt 401*
A. biflora Weimarck	32	Caledon, C.P. *Goldblatt 215*
A. juncifolia Bak.	32	Cape Point Reserve, C.P. *Goldblatt 480*
A. africana (L.) Hoffmg.	32	Steenberg Plateau, C.P. *Goldblatt 182*
A. glauca Klatt	32	Cape Point Reserve, C.P. *Goldblatt 396*
	64	Kenilworth, Cape Town, C.P. *Goldblatt 398*
PATERSONIA R. Br.		
P. occidentalis R. Br.	24	Perth (Australia), seed from Kings Park
NIVENIA Vent.		
N. levynsiae Weimarck	32	Buffelstaalberg, Rooi Els, C.P. *Goldblatt 464*
N. stokoei (Guthrie) N. E. Br.	32	Betty's Bay, C.P. *Goldblatt 407*
N. corymbosa (Ker) Bak.	32	Bains Kloof, C.P. *Goldblatt 185*
WITSENIA Thunb.		
W. maura Thunb.	32	Betty's Bay, C.P. *Goldblatt 407*
KLATTIA Bak.		
K. partita Bak.	32	Kogelberg, C.P. *Rourke 1186* (NBG)
BOBARTIA L.		
B. lilacina Lewis	20	Donker Kloof, Du Toit's Pass, C.P. *Esterhuysen 32376*
B. gladiata (L.f.) Ker.	20	Bains Kloof, C.P. *Goldblatt 412*
B. indica L.	20	Silvermine, C.P. *Goldblatt 400*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province – C.P.; Transvaal – Tvl. Specimens are housed in the Bolus Herbarium, Cape Town, unless stated to the contrary.

The chromosome counts for the other eight species studied in this work are new records. Of these, all but one proved to have a diploid number of 32.


A
B
C
D
E
F
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5
μ

The exception is a polyploid form of *A. glauca* with 64 chromosomes. It is clear that with about a quarter of the species in the genus having been investigated, the basic number of *Aristea* is 16.

Polyploidy in *Aristea*

Aristea ecklonii is an unusual species for it clearly has both polyploid and diploid races. All three geographically separate populations sampled by the author in South Africa, from the Transvaal to the eastern Cape Province, proved to be polyploid, while a Rhodesian population was diploid. Plants of the latter population were somewhat different morphologically from the southern ones, having much longer seed capsules. It is likely that the Rhodesian plants belong to a separate sub-species. The occurrence of polyploidy in *A. glauca* is also problematic. Two separate populations on the Cape Peninsula were studied and one proved diploid and the other polyploid. In view of the rarity of polyploidy in the Iridaceae in the south western Cape Province, it seems likely that the polyploid population is abnormal and may be a case of isolated autopolyploidy. The problem does, however, require further investigation.

PATERSONIA

$2n = 24.$

This is an Australian genus which appears to be allied to *Aristea*. It has a similar habit and vegetatic appearance, has blue to purple flowers but differs in having reduced or absent inner perianth segments. Only one species was examined. The chromosomes are comparatively small but there is a single pair of long chromosomes which give the karyotype a distinctive appearance. The chromosomes of this species are acrocentric and similar in appearance and size to *Aristea* except for the presence of the large pair of chromosomes (fig. 1:M).

NIVENIA

$2n = 32.$

Nivenia, together with *Witsenia* and *Klattia* comprise the so called woody or shrubby genera of the Iridaceae. They all have rather woody stems, lack modified rootstocks and exhibit secondary growth. *Nivenia* appears to be the least specialised of the group, having blue flowers and resembling *Aristea* in many ways. The flowers differ in having a short perianth tube.

Nivenia comprises eight species, three of which were examined cytologically by the author. All have a similar karyotype in which the diploid number is 32. The chromosomes are all acrocentric and small, ranging in size from 1 to 2μ.

Fig. 1.

Karyotypes of *Aristea* and *Patersonia*. A. *Aristea woodii;* B. *A. ecklonii;* C. *A. ecklonii* var.; D. *A. confusa;* E. *A. major;* F. *A. spiralis;* G. *A. monticola;* H. *A. bicolor;* I. *A. juncifolia;* J. *A. africana;* K, L. *A. glauca;* M. *Patersonia occidentalis.*

The chromosomes are very slightly larger than those found in species of *Aristea*, but except for this, the karyotypes are remarkably similar (fig. 2, A, B, C).

WITSENIA

2n = 32.

Witsenia is a monotypic genus found in the south western Cape Province. Although a woody plant, it is found only in marshy places that are moist all year round. *Witsenia maura* has a diploid number of 32. The karyotype is very similar to that of *Nivenia* and *Aristea* both in the size and general appearance of the chromosomes (fig. 2:D).

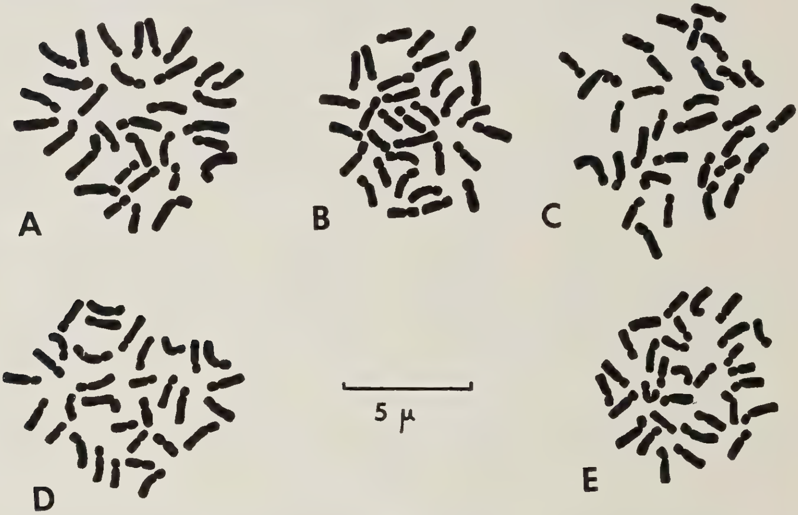

Fig. 2.

Karyotypes of *Nivenia*, *Witsenia* and *Klattia*. A. *Nivenia levynsiae;* B. *N. stokoei;* C. *N. corymbosa;* D. *Witsenia maura;* E. *Klattia partita.*

KLATTIA

2n = 32.

Klattia the third of the woody genera, is also confined to the south western Cape. There are two species in the genus, both found at fairly high altitudes in the mountains where the rainfall is fairly high. The flowers on the shrubby plants seem rather specialised. They are enclosed in the large brightly coloured bracts, and only the stamens and style appear beyond the bracts.

Only one of the two species, *Klattia partita* was studied. The diploid number is 32 and the karyotype is very similar to those of *Witsenia*, *Nivenia* and *Aristea* (fig. 2:E).

There have been no previous cytological reports on the above four genera. It is clear that the woody South African genera, *Nivenia*, *Klattia* and *Witsenia* have a basic number of 16 and have a karyotype very like that of *Aristea*. *Patersonia occidentalis*, the Australian species, has quite a different karyotype, but seems to share with *Aristea* and the other genera of the group a general similarity in the size and appearance of the chromosomes. This can perhaps be taken as evidence of its relationship to the South African genera, though probably this is rather distant.

The classification of *Aristea* and its allies.

Aristea and *Patersonia* have usually been treated as belonging to the same tribe or subtribe (Bentham & Hooker 1883). The woody or shrubby genera have been accorded the same treatment until recently, and in fact *Nivenia* was regarded as belonging to *Aristea* by Bentham & Hooker and Hutchinson. In his revision of *Aristea*, Weimarck (1940) discussed the systematic position of *Aristea* and its allies and concluded that the shrubby genera, *Patersonia* and others, were sufficiently distinct in having a perianth tube to be placed in a separate tribe from *Aristea* which he placed in the *Sisyrinchieae* (sensu Hutchinson). As Weimarck was following Bentham & Hooker's classification, he removed *Nivenia*, *Witsenia* and *Klattia* from the tribe *Aristeae* and placed them in the new tribe *Nivenieae* together with *Patersonia* and several South American genera. Lewis (1954) continued to recognise the woody genera as distinct and placed them alone in the *Nivenieae*, one of the three tribes she recognised, while referring *Aristea* to the tribe *Irideae* with *Homeria*, *Moraea* and their allies.

The cytological results do not support the treatments of either Weimarck or Lewis for it appears that *Aristea* and the woody genera form a natural unit and although *Patersonia* appears allied to this group it is more distantly related. The classification of Bentham & Hooker and of Hutchinson, who modified it only slightly, is generally in accord with the cytological evidence. Pax's treatment, however, seems the best for he placed *Aristea* and the woody genera in one subtribe and *Patersonia* in the other subtribe of the *Aristeae*.

As similarity in karyotype is evidence of genetic and consequently phylogenetic relationship it seems that no classification is tenable that does not recognise the relationship of *Aristea* to the woody genera. If the shrubby habit and secondary growth are regarded as justification for referring the woody genera to a distinct group then *Aristea* must be recognised as constituting a similar monotypic group of equal rank.

Weimarck's system would have *Aristea* in the *Sisyrinchieae*, while *Nivenia* etc. with the same karyotype as *Aristea*, are in another tribe. Lewis' system is untenable for the same reason. It appears then that Weimarck's reason for breaking up the old subtribe *Aristeae* on the basis of presence or absence of a perianth tube is not a good one, and that the perianth tube is not a character of great significance. The feature of secondary growth and shrubby habit used by Lewis in separating *Nivenia* and *Aristea* is also clearly not one of sufficient importance for the maintenance of the *Nivenieae* as a distinct tribe. *Aristea* and the shrubby genera must be admitted to the same tribe or subtribe but below this level it is only a matter of opinion whether further subdivision should be made to separate *Aristea* from the woody genera on the basis of presence or absence of secondary growth.

A study of the xylem elements in the Iridaceae by Cheadle (1964) is very significant, for the tribe *Aristeae* (*Aristea*, *Nivenia*, *Klattia* and *Patersonia*) was found to have the most primitive vessels in the family. Vessels are only found in the roots of Iridaceae except for *Sisyrinchium* and vary in length and nature of their perforation plates. Most of the family have specialised vessels but the *Aristeae* are the exception. This confirms the suggestion of other taxonomists that *Aristea* and its allies are the most primitive group in the family. The grouping of *Aristea*, the woody genera and *Patersonia* is also supported, while Weimarck's placing of *Aristea* with *Sisyrinchium* is shown to be incorrect.

Hence the cytological and anatomical evidence supports the maintenance of *Aristea*, the woody genera, and *Patersonia* in a single group. It is proposed that together with the South American genera which appear to be morphologically allied, they be placed in a single subtribe of the *Sisyrinchieae*, called the *Aristeineae*.

The occurrence of secondary growth in the *Monocotyledonae* is unusual, but is known in several genera. It was found by Scott & Brebnor (1893) and Adamson (1926) that secondary growth in *Nivenia*, *Klattia* and *Witsenia* resembled that found in other *Monocotyledonae*. The phylogenetic significance of the feature is not known. It was once regarded as the remnant of the primitive condition in the *Monocotyledonae* but can as equally be regarded as a secondary specialisation.

The geographical distribution of the woody genera is reminiscent of old relict populations for they occur in isolated groups on mountains, ravines or in marshes. They do not, however, appear to be primitive for they have rather specialised inflorescences and, except for *Klattia*, have flowers with a perianth tube. In view of the primitive nature of the vessels in these genera they cannot be regarded as very advanced, but are perhaps more specialised than *Aristea* from which they may have been derived.

Subtribe 2. ***Sisyrinchiineae***.

Only African representative: *Bobartia*.

This group is more specialised than the *Aristeineae*, having a rhizome, sometimes a modified, terete leaf and flowers with divided style branches.

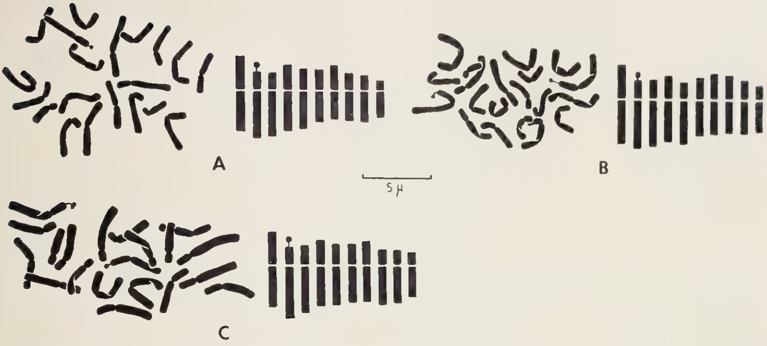

Fig. 3.
Karyotypes and idiograms of *Bobartia*. A. *Bobartia lilacina;* B. *B. gladiata;* C. *B. indica.*

BOBARTIA

Bobartia is a fairly small genus of about twelve species found throughout the winter rainfall region of the Cape Province. The plants are herbaceous, and possess a creeping, rhizomatous rootstock. The flowers have a short perianth tube, equal segments, and have a divided, three branched style. Typically, the flowers are yellow though one species has blue flowers.

Three species were studied by the author (Table 4). In all three a similar karyotype with a diploid number of 20 was found (fig. 3). The chromosomes are considerably larger than those found in *Aristea* and its allies and range in size from about 3—5 μ. The chromosomes are of sufficient size for details of the karyotype to be clearly visible and idiograms for all three species could be constructed. As can be seen in fig. 3, the karyotypes are remarkably similar. The longest chromosome pair is metacentric in all three species and the second longest pair bears a small satellite at the end of the shorter arm of the chromosome.

There are two distinct growth forms in the genus. Two species have a narrowly ensiform leaf and a much ramified paniculate inflorescence. One of the species studied here, *B. lilacina*, has this habit (Lewis 1945). A peculiarity of these two species is the presence of a sticky material found below each node of the aerial part of the plant. This feature occurs in the tribe *Irideae* in a few species of several genera, e.g. *Moraea*, *Homeria* and *Ferraria*.

The other type of growth form in *Bobartia* is clearly more specialised. The leaves are linear or terete, and the inflorescence condensed so that the scape is unbranched and the flowers grouped in a compact head. It has been suggested that the two growth forms are so different that *Bobartia* should be divided into two genera on these grounds. While there is some merit in the argument, the floral morphology is very similar in both groups. The cytology is similar in both, and confirms that they are closely related. It is more a question of convenience as to whether the genus should be divided. Because the genus is small, and the two unusual branched species can be very easily recognised, it does not seem necessary to alter their present taxonomic treatment.

Bobartia belongs to the tribe *Sisyrinchieae* which, as already mentioned, characteristically has small chromosomes. Though *Bobartia* at first seems to prove an exception, a closer examination of the general chromosome size in this genus as compared with species in the *Irideae* shows that chromosomes are more slender and significantly smaller than, for example, in *Dietes* where a diploid number of 20 is also found. *Bobartia* appears to be intermediate between the small and large chromosome groups. The difference in chromosome size between it and the remainder of the genera in the *Sisyrinchieae* that have been studied seems significant and *Bobartia* is clearly only distantly related to *Aristea* and its allies.

The anatomy of the xylem elements has been mentioned in the section on *Aristea* where it was shown that *Aristea* and its allies have the most primitive vessels in the family. *Bobartia* does not belong to this group for it has the relatively specialised vessels typical of the rest of the family. In *Sisyrinchium*, suggested by some authors to be a close ally of *Bobartia*, specialised xylem vessels occur in aerial parts of the plant as well as the roots. This genus is anatomically the most specialised in the family, but there is no indication that *Bobartia* has any vessels in its stems and leaves.

Morphologically *Bobartia* and *Sisyrinchium* appear intermediate between the *Aristea* group and the *Irideae*. In both the rootstock is a rhizome, the leaves equitant and usually ensiform and the inflorescence consists of a number of small cymes (or rhipidia) each containing two usually fugaceous flowers enclosed in large bracts or spathes. The main difference between the groups is that the flower usually has a perianth tube in *Aristeineae* (but not in *Aristea*) and the style is always undivided, but in the *Sisyrinchieae*, the perianth tube is always absent and the style is divided into 3 long branches. In some genera of the *Irideae*, the vegetative features are similar but the flowers have a branched style with forked or divided stigmas and, more significant, they have the style branches opposite the stamens and not alternate as in the rest of the family. Apart from this, the *Irideae* have very large chromosomes which serve to emphasise the distinctness of this group.

As can be seen, *Bobartia* (and perhaps other members of the *Sisyrinchieae*), is to some extent intermediate between the primitive *Aristeineae* with unspecialised morphology and anatomy, and with very small chromosomes, and the more advanced *Irideae* with their more specialised flowers, and often other modified morphological features, with very large chromosomes. If the tribe *Sisyrinchieae* is to remain recognised, *Bobartia* and *Aristea* and its allies must be placed in separate subtribes. The difference between these two subtribes does, however, seem greater than between the other subtribes that are recognised by the present author, and perhaps *Aristea* and *Bobartia* should be placed in separate tribes. More genera in the *Sisyrinchieae* (sensu lato) should be examined recognise two tribes here and until then *Bobartia* should be placed in the subtribe *Sisyrinchieae*.

4.3 Tribe 2. *IRIDEAE*

The tribe *Irideae* comprises plants often more modified than the *Sisyrinchieae*. The rootstock is either a rhizome, bulb or corm and the leaves equitant or secondarily bifacial. The inflorescence, a cyme, enclosed in large spathe-like bracts, is similar as is the fugaceous habit of the flowers. These are, however, often modified by reduction or difference of the inner perianth segments and the style and style branches are usually elaborate. The tribe is world wide in distribution, the best known genus being *Iris*. The African genera are *Dietes*, *Moraea*, *Gynandriris*, *Homeria*, *Hexaglottis*, *Galaxia* and *Ferraria*.

THE CYTOLOGY, CYTOTAXONOMY AND POSSIBLE PHYLOGENY OF THE SOUTH AFRICAN GENERA.

a. The genus ***Dietes***

2n = 20, 40.

Dietes comprises about six species of fairly large herbaceous plants. The rootstock is a woody, creeping rhizome, the leaves long, equitant and firm and the inflorescence a tall, fairly branched structure bearing clusters of flowers at the apices of the branches. The flowers are similar to those of *Iris* with large outer and smaller inner perianth segments and a large petaloid and branched style. The flowers differ in lacking a perianth tube and the inner segments are spreading and not erect as in most species of *Iris*. The genus has a peculiar distribution in that five species occur along the south east coast of Africa while the sixth is found in eastern Australia and Lord Howe Island.

The cytology of four of the six recognised species was investigated (Table 5). In three, *Dietes vegeta*, *D. grandiflora* and *D. butcheriana*, a diploid number of 20 was obtained, but *D. bicolor*, with a somatic number of 40 appears to be polyploid. The karyotypes of all the species are fairly similar and are characterised by having several metacentric chromosomes (fig. 4: A—F). This is perhaps closest of all the genera studied by the author to the symmetric karyotype of Stebbins (1950), in which there are several metacentric chromosomes, and no great difference in size occurs between the chromosomes. This karyotype is frequently correlated with primitive characters and is believed to be less specialised than the asymmetric karyotype in which acrocentric chromosomes occur.

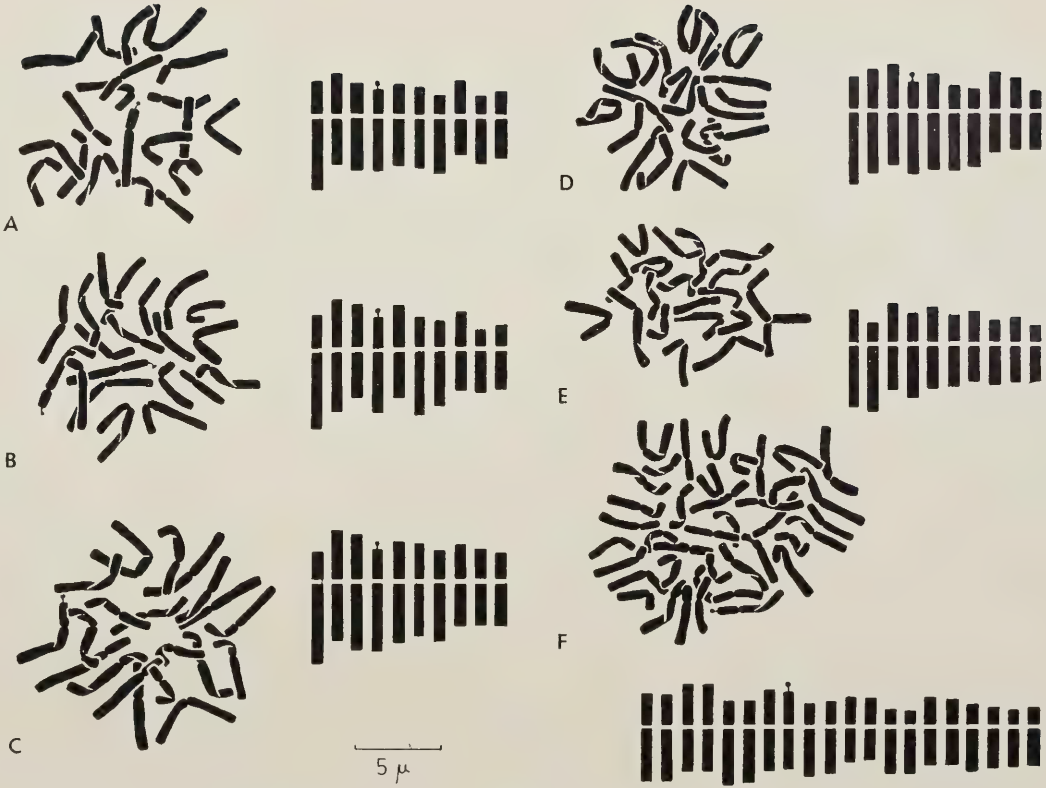

FIG. 4.

Karyotypes and Idiograms of *Dietes*. A. *Dietes vegeta* from Inanda, Natal; B. *D. vegeta* from Inhaca Island; C. *D. vegeta* from Haenertsburg; D. *D. grandiflora;* E. *D. butcheriana;* F. *D. bicolor.*

Three separate geographical races of *Dietes vegeta* were examined. In the past these three types were recognised as two different species and a variety (Brown 1928) but are now considered a single species (Obermeyer 1969). The karyotypes of the geographical races were found to vary little, and resembled one another more closely than those of the other species studied (fig. 4: A, B, C). This degree of intraspecific variation in the karyotype is to be expected in widely separate populations or races and tends to confirm the placing of these in a single species.

The present study confirms the finding of Sharma & Sharma (1960) and Sakai (1952) who obtained a diploid number of 20 in *Dietes vegeta* (known to them as *Moraea iridioides* var. *johnsonii*). Riley (1962) also reported a diploid number of 20 in this species (as *D. prolongata*). The karyotypes found by these workers appear to be similar to those found by the present author and fit within the limits of karyotypic variation for *D. vegeta.*

TABLE 5
Chromosome numbers in *Dietes* and *Gynandriris.*

Species	Diploid No.	Collection Data or Reference
DIETES		
D. vegeta (L.) N.E. Br. . . .	20	Inanda, Natal. *Mauve 4443* (PRE)
	20	Inhaca, Mocambique. *Goldblatt 91* (J)
	20	Haenertsburg, Tvl. *Goldblatt 381.*
(as Moraea iridioides var. johnsonii)	20	(Sakai 1952)
(as D. iridioides var. johnsonii)	20	(Sharma & Sharma 1960)
(as D. iridioides var. mcleyii) .	40	(Sharma & Sharma 1960)
(as D. prolongata)	20	(Riley 1962)
D. grandiflora N.E. Br. . . .	20	Natal (ex. hort) *Goldblatt 46* (J)
D. butcheriana Gerstner . . .	20	Noodsberg, Natal. *Strey 4875* (PRE)
D. bicolor (Lindl.) Sweet . .	40	Eastern Cape (ex. hort.) *Goldblatt 35* (J)
(as D. iridioides var. bicolor) .	40	(Sharma & Sharma 1960)
GYNANDRIRIS		
G. sisyrinchium (L.) Parl. . .	24	Europe (Simonet 1932)
G. setifolia (L.f.) Foster . . .	12	Villiersdorp-Worcester Rd., C.P. *Goldblatt 208.*
G. torta (L. Bol.) Foster . . .	12	Nieuwoudtville, C.P. *Goldblatt 273.*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province – C.P.; Transvaal – Tvl. Specimens are housed at the Bolus Herbarium unless stated to the contrary.

Sharma & Sharma also reported finding a diploid number of 40 for both *Moraea iridioides* var. *mcleyii* (presumably a horticultural variety of *Dietes vegeta*) and *M. iridioides* var. *bicolor* (*D. bicolor*). This latter count is confirmed by the present study. *Dietes bicolor* seems to be a tetraploid species, and apparently an allopolyploid, as the chromosomes can be matched in pairs but not in fours. Meiosis in this species was examined and found to be normal and all the plants examined were fully fertile. On the assumption that the species is allopolyploid, an attempt was made to discover its ancestry by crossing it with *D. vegeta*, the only species which occurs in the same natural locality. A cross between *D. bicolor* and *Moraea ramosissima* a species with a similar karyotype was also attempted but both crosses proved unsuccessful.

The chromosome counts for *D. grandiflora* and *D. butcheriana* are new records and tend to confirm the suggestion that the basic number for *Dietes* is 10.

The taxonomic position and phylogenetic significance of *Dietes*.

Dietes is a genus belonging to the tribe *Irideae* and it has the long chromosomes typical of this group. The distribution of the genus is peculiar as five of the species occur in southern Africa from the Cape Province to Malawi and the remaining species is found in southern Queensland and on Lord Howe Island off the east coast of Australia. *Dietes* is allied to *Iris* and *Moraea* and has been included within both genera at one time or another. It was considered by Baker (1896) and Cahen (1943) to be a subgenus of *Moraea*. The latter author suggested that the recognition of *Dietes* as a genus on the grounds of its rhizomatous rootstock, would be inconsistent with the treatment accorded to *Iris*. Cahen had, however, an incomplete understanding of *Dietes* and did not realise it differed in other respects from *Moraea*. The present author believes that *Dietes* is intermediate between *Iris* and *Moraea* and cannot thus be correctly incorporated within either genus. It shares with them the characteristic double-crested petaloid style branches but it also has a number of features which can be regarded as more primitive than those in *Iris* and *Moraea*: the rootstock is a creeping rhizome; the leaves are equitant; the scape very ramified and the flowers have spreading perianth segments, no perianth tube and free stamens (fig. 5: A).

Iris and *Moraea* have diverged from this basic type in two directions. The rootstock in *Iris* has remained a rhizome or has been modified to form a bulb, the branching is reduced and the flowers have a perianth tube. In the bulbous species of *Iris* the leaf has also become modified and is bifacial with only the apex equitant. In *Moraea* the rootstock is a corm, the branching is reduced in many species and while the flower has no perianth tube (except in a single species), the filaments in most species are connate and form a column round the base of the style. The leaves in *Moraea* are bifacial but in many species the apex is

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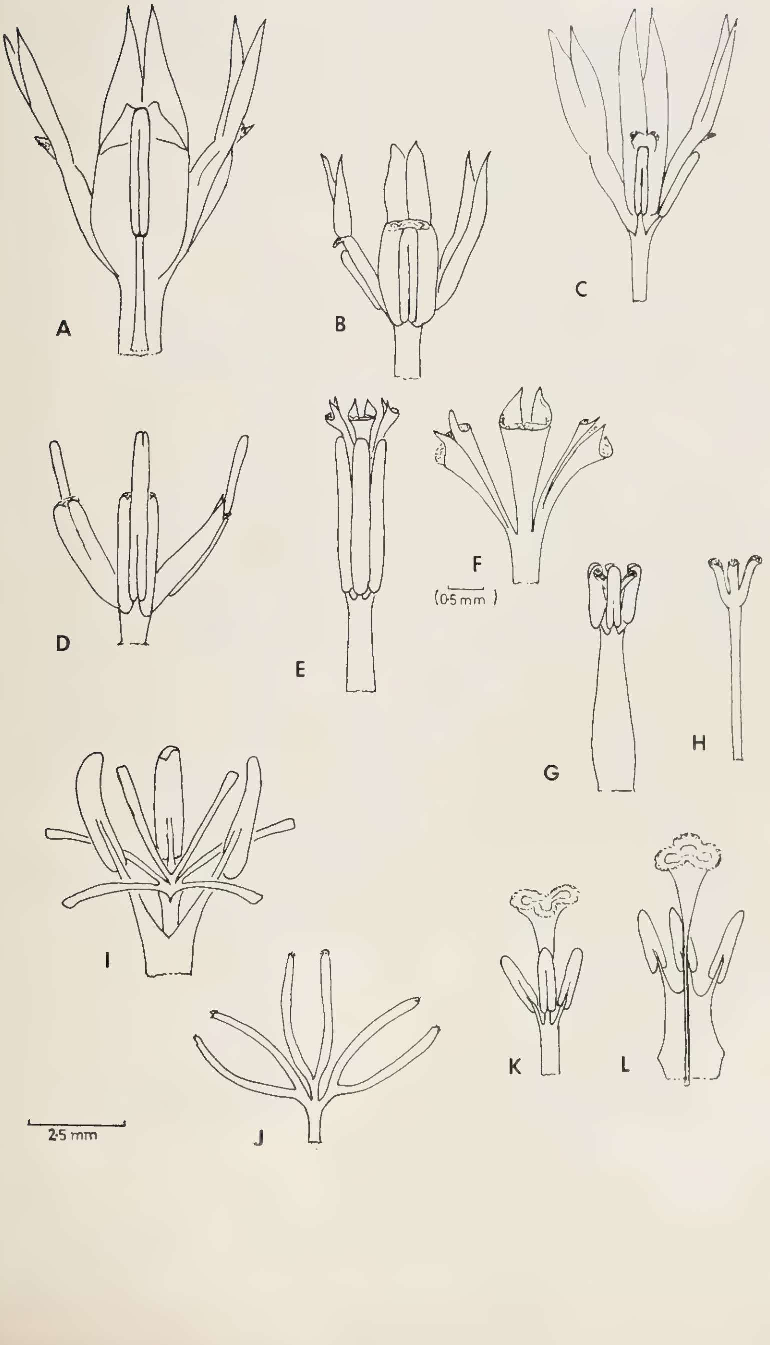
FIG. 5.

The structure and arrangement of the stamens, style and stigma in the South African representatives of the *Irideae*. A. *Dietes vegeta;* B. *Moraea macronyx;* C. *M. villosa;* D. *M. gigandra;* E. *Homeria breyniana;* F. *H. breyniana* with style partly dissected; G. *H. miniata;* H. *H. miniata* style with stamens removed; I. *Hexaglottis virgata;* J. *H. sp.* showing style branches in detail; K. *Galaxia ovata;* L. *G. ovata* partly dissected.


A
B
C
D
E
F
(0·5 mm)
G
H
I
J
K
L
2·5 mm

equitant. It is believed that the so-called leaf is in this case an extended leaf sheath, which explains its bifacial nature and the equitant tip would thus be the vestigial remains of the true leaf (Arber 1921, Lewis 1954).

Iris is widely distributed throughout the northern hemisphere while *Moraea* is an African genus occurring mainly south of the equator with the greatest concentration of species in the south western Cape Province. It is believed that the two genera developed independently in different areas, but apparently from a common ancestor very like *Dietes* if not that genus itself. If this theory is correct it would be expected that the basic or primary chromosome number in both *Moraea* and *Iris* would be 10. Diploid numbers of 20 do in fact occur in these genera, both of which are heteroploid. The idea that this number is primitive may prove helpful in unravelling complexities of evolution in *Iris* and *Moraea.*

b. The genus *Moraea*

2n = 12, 18, 20, 24.

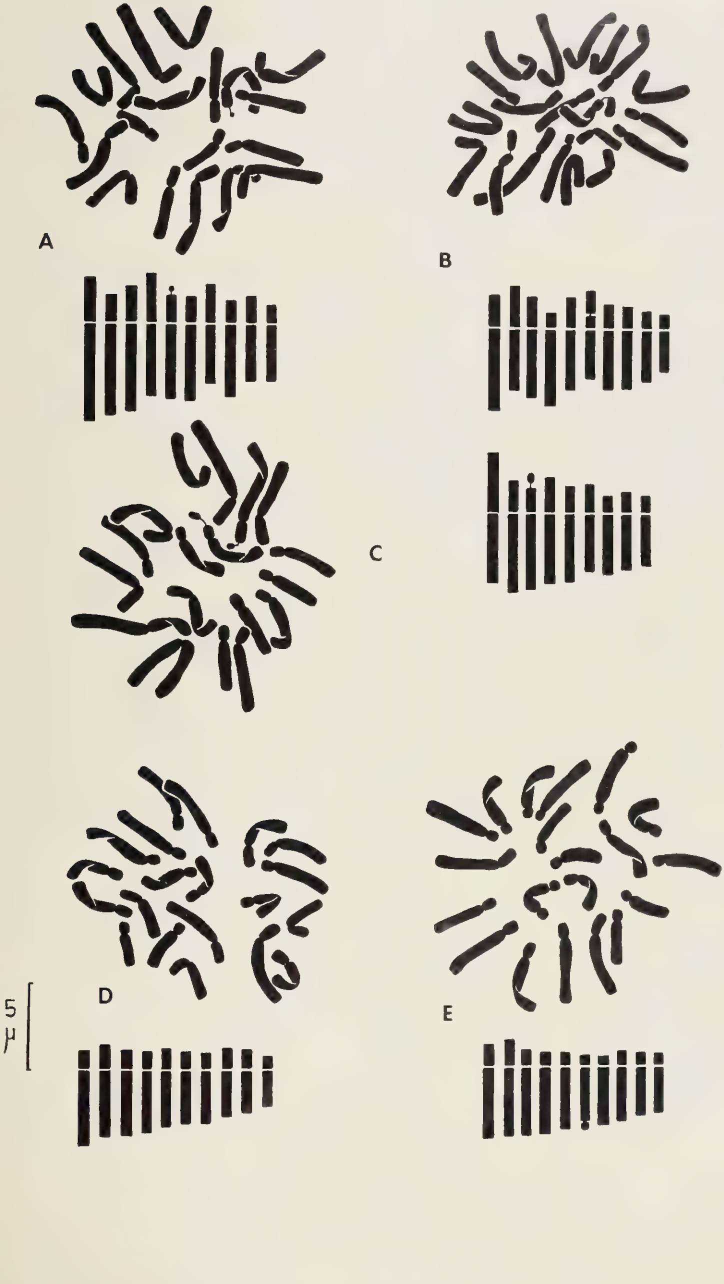
The genus *Moraea* is a comparatively large one, comprising an estimated 60 species. The genus is distributed throughout sub-Saharan Africa with increasing frequency southwards; the greatest concentration of species being in the south western Cape Province. The plants are herbaceous and usually quite small. The rootstock is a corm consisting of an enlarged lateral bud and the leaves are bifacial instead of the usual monofacial type found in the family. The flowers are much like those of *Iris* and have large petaloid styles, the difference being that *Moraea* generally lacks a perianth tube and the filaments are contiguous and usually connate.

Twenty-five species, which reflect a fairly large sample of the total number, were studied by the present author. Large chromosomes were found in all species, but considerable variation in karyotype was observed. Diploid numbers of 20 and 12 are most common with 18 and 24 also occurring.

The species that were examined have been arranged after the system of Baker (1896) and as can be seen, different diploid numbers are sometimes observed in the same section. (Table 7). This is probably indicative of certain errors in the system. The karyotypes of the species will be discussed briefly as idiograms are given for each species and these give a more accurate impression of each karyotype than a verbal description. For purposes of comparison, the species are discussed in groups having similar karyotypes and not according to Baker's system.

Fig. 6.

Karyotypes and idiograms of *Moraea*. A. *Moraea ramosissima;* B. *M. odorata;* C. *M. papilionacea;* D. *M. neglecta;* E. *M. angusta.*


A
B
C
D
E
5 μ

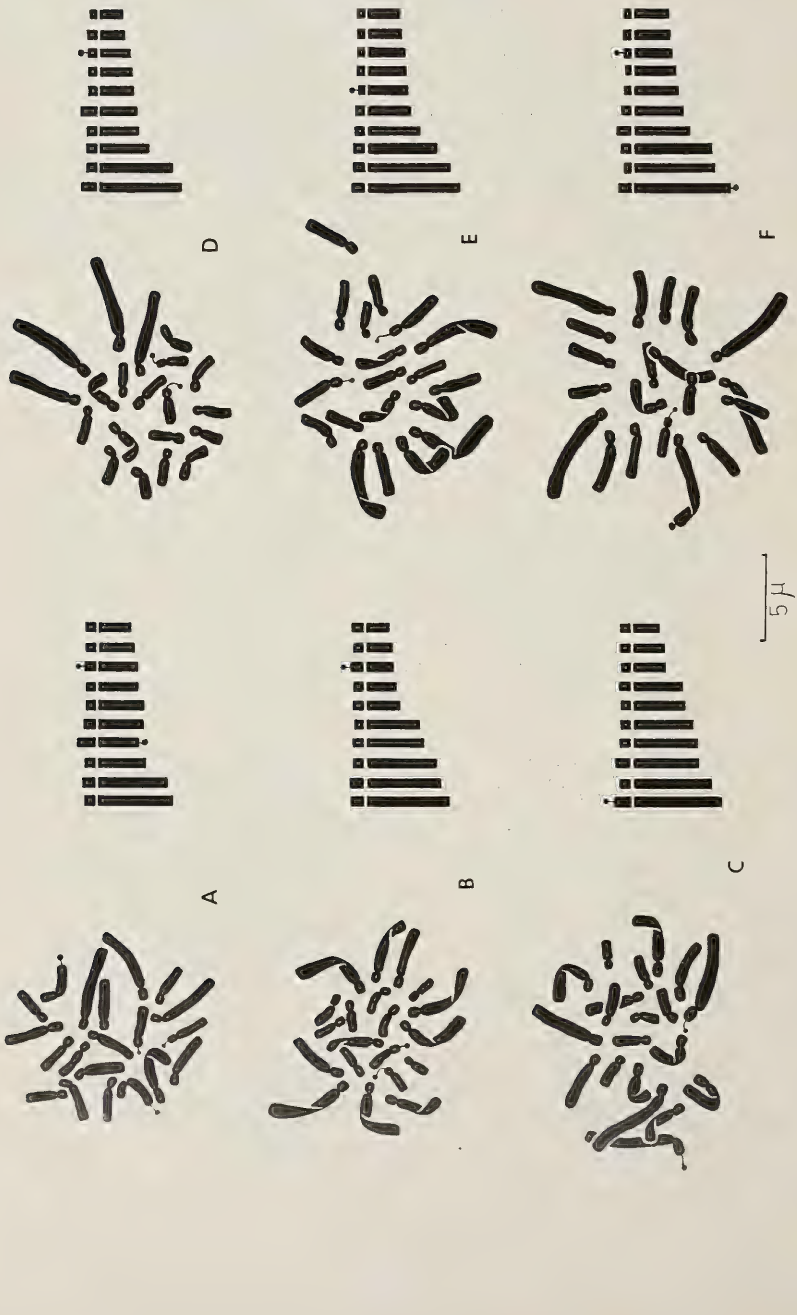


FIG. 7.
Karyotypes and idiograms of *Moraea*. A. *Moraea cooperi*; B. *M. framesii*; C. *M. juncea*; D. *M. gawleri*; E. *M. ciliata*; F. *M. macronyx*.

Of the species with a diploid number of 20, *M. ramosissima* and *M. odorata* appear to have the least specialised karyotypes if the view of Stebbins (1950) is accepted that the symmetrical karyotype with many metacentric chromosomes is primitive and unspecialised (fig. 6: A, B). In both species the variation in size is comparatively less than other species with 20 somatic chromosomes and there are two pairs of metacentric chromosomes in *M. odorata* and three in *M. ramosissima.*

The diploid number is 20 in *M. angusta* and its close ally *M. neglecta*, but here the karyotype is less symmetrical for there is a greater range in size and there are no metacentric chromosomes (fig. 6: D, E).

Moraea cooperi, *M. juncea*, *M. framesii*, *M. gawleri*, *M. ciliata* and *M. macronyx*, all having a diploid number of 20 appear to form a natural unit judging from the karyotype which is quite asymmetric here (fig. 7). All the chromosomes are acrocentric and there is considerable difference in size between the large and small chromosomes. The difference is least in *M. cooperi* which appears intermediate between this group and *M. angusta* in its karyotype. The remaining five species with this asymmetrical karyotype have chromosomes of similar sizes and have three or four pairs of larger chromosomes and the remaining pairs quite small. They differ, however, in having satellites on different pairs of chromosomes.

Moraea papilionacea seems unique in having a diploid number of 18 but it appears to be related to the species with the rather symmetric karyotype with 20 somatic chromosomes (fig. 6: C). The karyotype in this species is also rather symmetrical with a pair of metacentric and several pairs of submetacentric chromosomes.

The species with 12 or 24 chromosomes can also be divided into groups with symmetric and asymmetric karyotypes. *Moraea diphylla*, *M. fugax*, *M. insolens*, *M. polystachya*, *M. tripetala* and *M. trita* (apparently a tetraploid) all have at least one pair of almost metacentric chromosomes as in *M. polystachya* and even four pairs as in *M. diphylla* (fig. 8). There is no very great similarity in any of the karyotypes, as can be seen from the different positions of the satellites, the number of metacentric chromosomes and the variation in size, which is small in *M. polystachya* but considerable in *M. fugax*.

Moraea lurida, *M. bellendenii* and *M. villosa* all have karyotypes comparable to those of the previous group (fig. 11: A, B, C). *M. villosa* seems to be a polyploid species. Three geographically isolated populations were examined and all were found to have a somatic number of 24. The above three species are mentioned separately as they belong to a group accorded subgeneric rank by Baker. In these species the longest chromosome is conspicuously metacentric and at least in *M. bellendenii* and *M. villosa* can be seen to bear a small satellite at its one end.

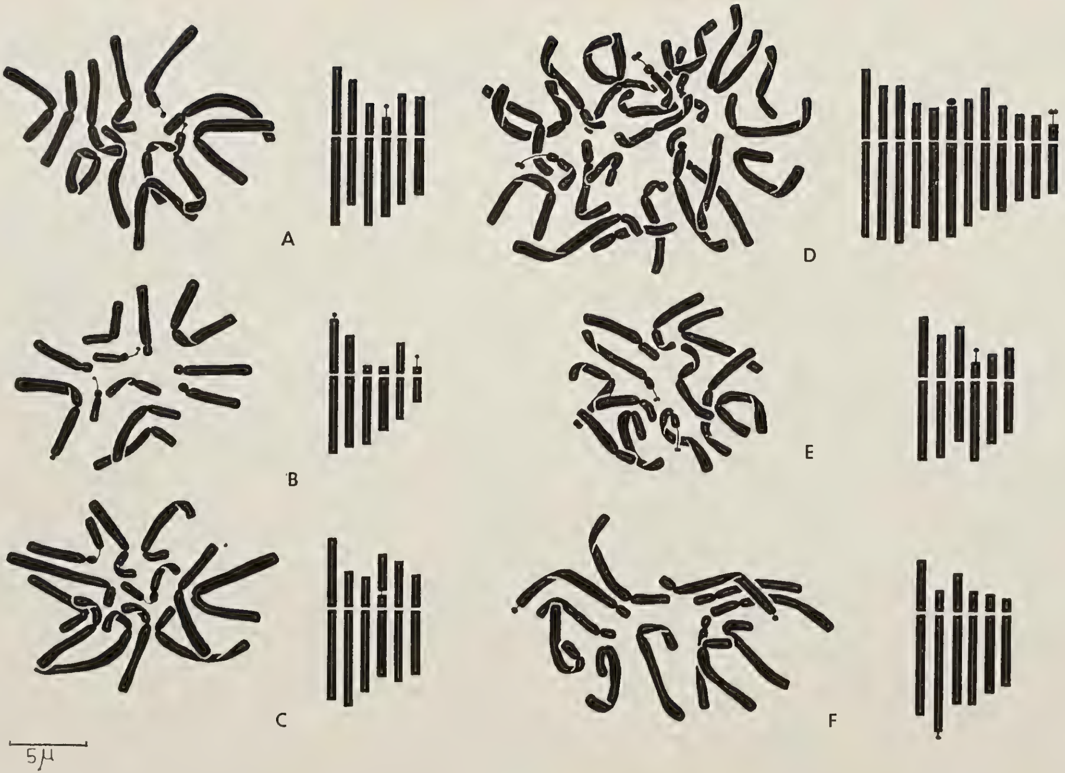


FIG. 8.
Karyotypes and idiograms of *Moraea*. A. *Moraea diphylla;* B. *M. fugax;* C. *M. insolens;* D. *M. trita;* E. *M. tripetala;* F. *M. polystachya.*

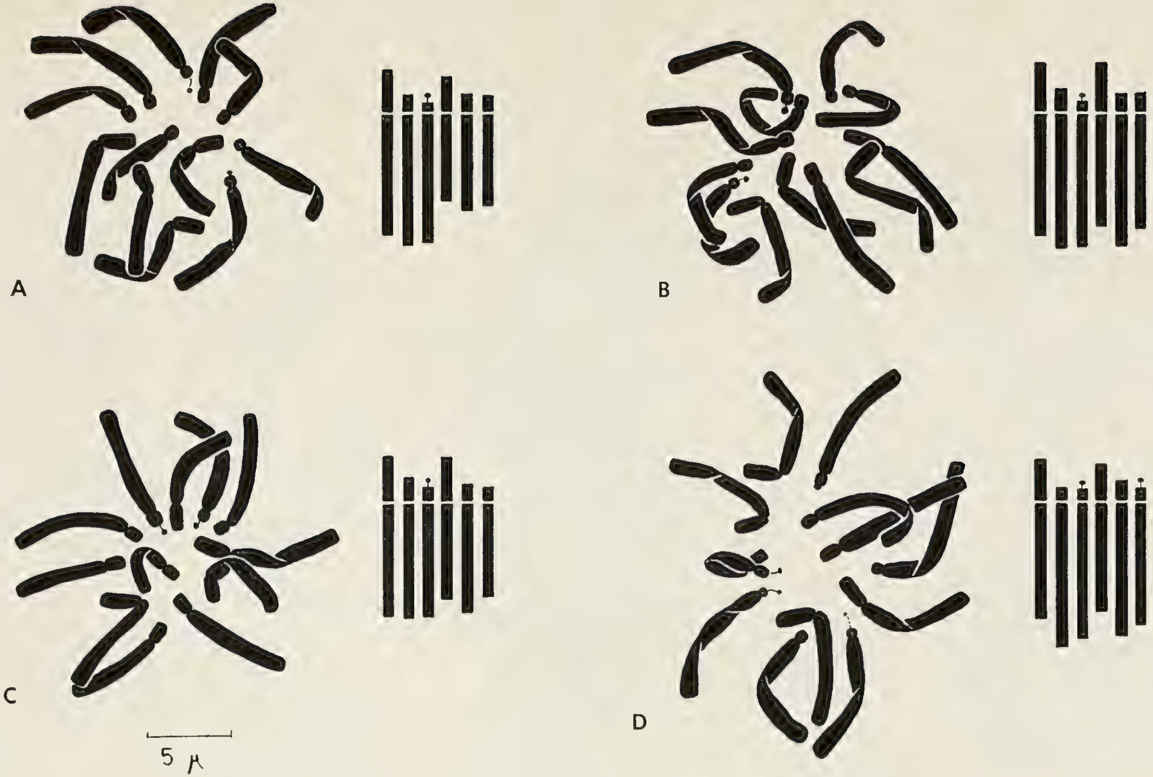


Fig. 9.

Karyotypes and idiograms of the *Moraea spathulata* complex. A. *Moraea spathulata* from Harrismith, O.F.S.; B. *M. spathulata* from Graskop, Transvaal; C. *M. spathulata* from Knysna, Cape Province; D. *M. sp. aff. moggii* from Lochiel, Transvaal.

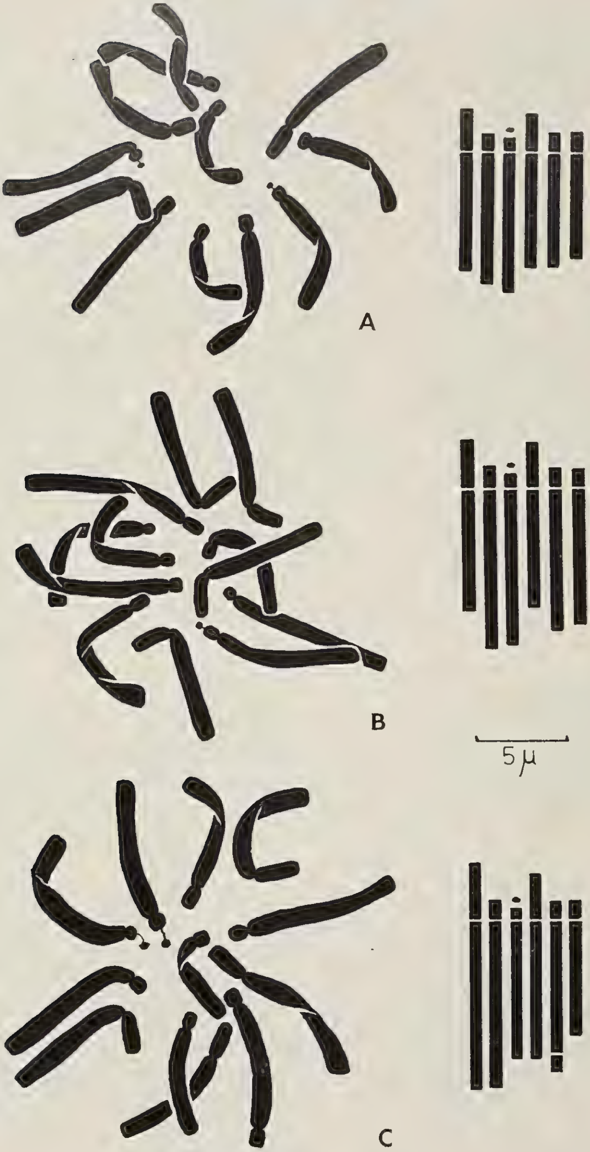


FIG. 10.
Karyotypes of *Moraea*. A. *Moraea rivularis;* B. *M. graminicola;* C. *M. schimperi.*

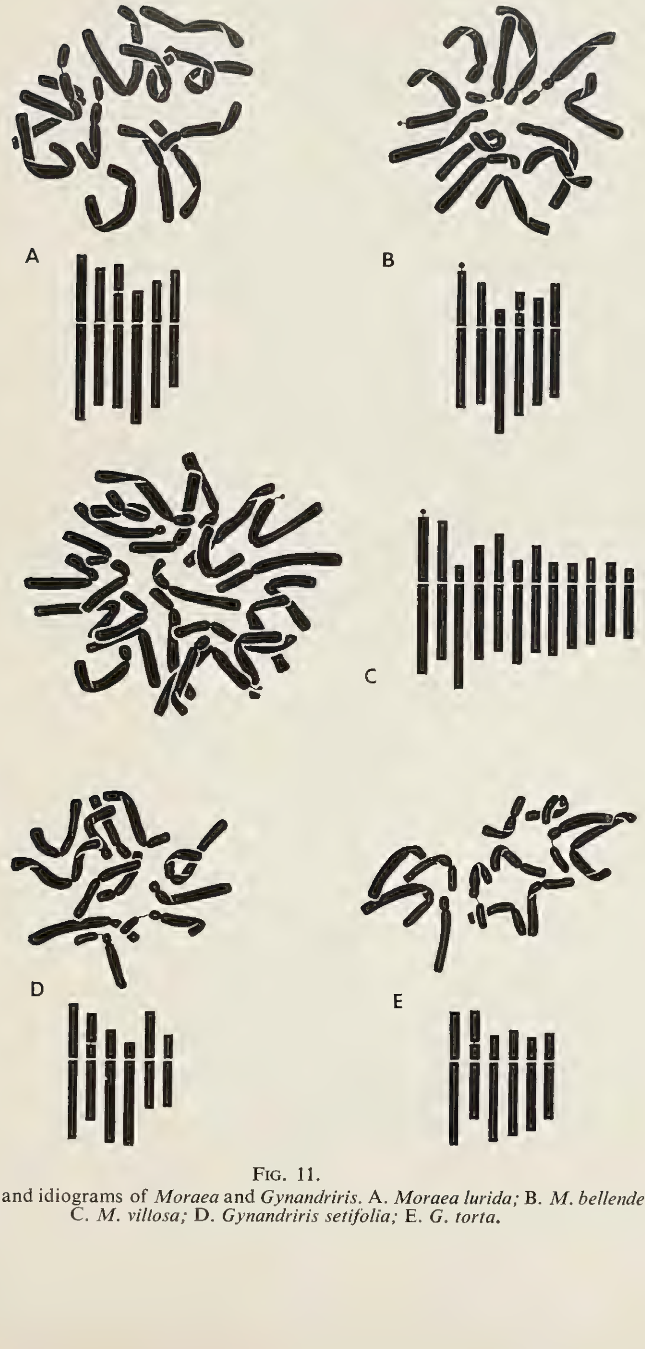


Fig. 11.
Karyotypes and idiograms of *Moraea* and *Gynandriris*. A. *Moraea lurida;* B. *M. bellendenii;* C. *M. villosa;* D. *Gynandriris setifolia;* E. *G. torta.*

The remaining species, *M. spathulata* and its allies, with 12 chromosomes all have a very similar karyotype. The chromosomes are very large and mostly acrocentric (fig. 9, 10). The longest and fourth longest pair are submetacentric and the third longest pair bear a small satellite at the end of the shorter arm. *M. spathulata* is itself a very widespread species extending from George in the Cape Province to the northern Transvaal. Three populations were examined from different areas and all were found to have a similar, but to a small extent different karyotype. It seems that small variations in karyotype do occur in species and may not have taxonomic significance. A similar conclusion was reached by Pienaar (1963) for the genus *Ornithogalum*.

There have been several earlier cytological reports on species of *Moraea*. Sakai (1952) reported a diploid number of 20 in *M. ramosissima* and 28 in *M. fugax* (as *M. edulis*). The first is confirmed by the present author although a rather different karyotype was recorded. The second count is, however, quite different from present observations and it is suggested that a mistake in identification of Sakai's plant was made. Fernandes and Neves (1961) reported a diploid number of 20 in *M. juncea* and Riley (1962) found 12 somatic chromosomes in *M. polystachya* and *M. spathulata*. These reports are confirmed by the present author. Lewis (1966) found a diploid number of 12 in both *M. erici-rosenii* and *M. spathacea*, and described the karyotypes as similar to that found by Riley for *M. spathulata*. These species have not been examined by the present author as they were not available. Apart from the five counts confirmed by the present author, there are 20 new cytological records for the genus.

The correlation of cytology and morphology.

The species of *Moraea* having a diploid number of 20 can be divided into three groups based on morphological criteria. The first group which corresponds to the section *Corymbosae* (subgenus *Moraea*) according to Baker (1896), consists of the plants which have a much ramified inflorescence and bear from three to several basal leaves. The karyotype in this group varies to some extent, ranging from that of *M. ramosissima* with rather large chromosomes, several of which are metacentric to *M. decussata* where an asymmetrical karyotype with both large and rather small acrocentric chromosomes occur.

The second group, corresponding to Baker's section *Acaules* comprises rather reduced species where the stem is unbranched and is rather short and enclosed by the three to several basal leaves. Only two of the five species in this section, *M. ciliata* and *M. macronyx*, were examined and these were found to have a karyotype very much like *M. juncea* and *M. gawleri*, both belonging to the previous section, *Corymbosae*. These latter two species are small and *M. juncea* particularly, has a short stem and few branches. It can thus be

TABLE 6

Chromosome numbers in *Moraea*. The arrangement and classification are after Baker (1896.)

Species	Diploid No.	Collection Data or Reference.
Subgenus 1. Moraea		
Section Corymbosae		
M. ramosissima (L.f.) Druce	20	Stellenbosch, C.P. *Goldblatt 50* (J)
	20	(Sakai 1952)
M. odorata Lewis	20	Quoin Point, C.P. *Goldblatt 478*
M. cooperi Bak.	20	Caledon district, C.P. *Goldblatt 440*
M. juncea L.	20	Groot Constantia, C.P. *Goldblatt 474*
	20	(Fernandes & Neves 1961)
M. framesii L. Bolus	20	Van Rhyns Pass, C.P. *Goldblatt 270*
M. gawleri Spreng (=decussata, or crispa)	20	Cape Point Reserve, C.P. *Goldblatt 502*
M. polystachya (Thunb.) Ker	12	Beaufort West, C.P. *Goldblatt 88 (J)*
	12	Graaff Reinet, C.P. *Goldblatt 221*
	12	(Riley 1962)
Section Acaules		
M. ciliata (L.f.) Ker	20	Nieuwoudtville, C.P. *Goldblatt 256*
M. macronyx Lewis	20	Calvinia district (ex hort) 144 (J)
Section Brevicaules		
M. papilionacea (L.f.) Ker	18	Tulbagh Rd., C.P. *Goldblatt 193*
	18	Constantia Nek, C.P. *Goldblatt 445*
Section Monocephalae		
M. angusta (Thunb.) Ker	20	Malmesbury Rd., C.P. *Goldblatt 444*
M. neglecta Lewis	20	Elim, C.P. *Goldblatt 361*
M. spathulata (L.f.) Klatt	12	Harrismith, O.F.S. *Naude s.n.* (*PRE 30038*)
	12	Graskop, Tvl. *Goldblatt 14 (J)*
	12	Knysna, C.P. *Goldblatt 26 (J)*
	12	(Riley 1962)
(as M. spathacea)	12	(Lewis 1966)
M. sp. aff. moggii N. E. Br.	12	Lochiel, Tvl. *Goldblatt 86 (J)*
M. erici-rosenii	12	(Lewis 1966)
M. graminicola Oberm.	12	Mooi River, Natal. *Mauve 4466* (PRE)
M. schimperi (Hochst) Pichi Sermolli	12	Nyika Plateau, Malawi. *Goldblatt 40 (J)*
M. lurida Ker	12	Klein Hagelkraal, C.P. *Goldblatt 363*
Section Subracemosae		
M. diphylla Bak.	12	Giftberg, C.P. *Goldblatt 207*
M. fugax (de la Roche) Jacq. (=M. edulis)	12	Hopefield, C.P. *Goldblatt 152* (J)
(as M. edulis)	28	(Sakai 1952)
M. trita N. E. Br.	24	Johannesburg, Tvl. *Goldblatt 155*
Subgenus 2. Vieusseuxia		
M. insolens Goldblatt ined.	12	Caledon, C.P. *Barnard s.n.* (NBG 87509)
M. bellendenii (Sweet)	12	Napier, C.P. *Goldblatt 338*
M. villosa Ker	24	Tulbagh, C.P. *Goldblatt 22*
	24	Riebeeck Kasteel, C.P. *Goldblatt 503*
M. tripetala (L.f.) Ker	12	Nieuwoudtville, C.P. *Goldblatt 101*

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suggested that there is a tendency for reduction in size and branching in the *Corymbosae* which leads through *M. juncea* to the *Acaules*. The relationship between this group and the smaller members of the *Corymbosae* is evidenced by the similarity of the karyotype.

The third group of species of *Moraea* with a diploid number of 20 consists of *M. angusta* and *M. neglecta*. These are also apparently modified from the *Corymbosae* but here the aerial stem is well developed and the branching is reduced and usually absent. The number of leaves is fewer, and there is often only a single basal leaf. These two species were placed by Baker in the section *Monocephalae* characterised by an unbranched stem with a terminal cluster of flowers. The remaining species that he referred to in this group were found to have a diploid number of 12.

Only one species, *M. papilionacea* was found to have a diploid number of 18. This and *M. fimbriata* (not examined) comprise Baker's section *Brevicaules*, characterised by plants with short but branching stems and several basal leaves. The karyotype of *M. papilionacea* seems to be most similar to *M. ramosissima* in size and appearance of the chromosomes but of course there is a reduction in number. *Moraea papilionacea* appears to be allied to the *Corymbosae* but may be a link between that group and the species of *Moraea* having a diploid number of 12.

Those species of *Moraea* with 12 or 24 somatic chromosomes can also be divided into groups based on their morphology. The first of these corresponds to Baker's section *Subracemosae* which comprises plants with two, or more often, only one basal leaf and stem bearing only a few short branches. In this group, which includes *M. fugax*, *M. diphylla* etc., the karyotype is characterised by having one or two metacentric chromosomes.

A second group is the remainder of Baker's *Monocephalae*. As characterised by *M. spathulata*, these species have a single leaf and unbranched inflorescence. Here the karyotype seems more asymmetric than in the previous group for there are no metacentric chromosomes. As is so often observed, the asymmetry of the karyotype is associated with morphological specialisation and species in this group are clearly among the most reduced or modified in the genus.

The third group with a base number of 6 corresponds to Baker's separate subgenus, *Vieusseuxia*. In this group the vegetative features seem to be relatively specialised for there are only one or two leaves and the stem is little branched. The group was given subgeneric status because of the modification of the flower. The inner perianth segments are very small and often tricuspidate or sometimes almost vestigial. Here the karyotype consists of rather large chromosomes, several of which are metacentric.

The value of the criteria on which Baker based this last group appears rather doubtful. *Moraea cooperi* ($2n = 20$), placed in error by Baker in the *Corymbosae* (according to his criteria), actually lacks inner perianth segments and should thus be considered as belonging to the subgenus *Vieusseuxia*. Clearly the plant would be misplaced here for it is much branched and the karyotype is like that in other members of the *Corymbosae* where it should remain, though this group must be redefined.

The *Moraea tripetala* was one species included in *Vieusseuxia* by Baker because it had very reduced inner perianth segments. It is perhaps misplaced here as it is unlike most other members of this subgenus which usually have very broad, oval outer segments and tricuspidate inner segments. The reduction of the inner segments in *M. tripetala* may be an independent change comparable to that in *M. cooperi* which is clearly well placed in the section *Corymbosae*. The outer perianth segments in *M. tripetala* are lanceolate with a raised midline and down-turned edges, like those in the subgenus *Moraea*. Its diploid number of 12 and moderately branched habit suggest the features of the section *Subracemosae* to which it may be better referred.

The two other subgenera of *Moraea* proposed by Baker were *Helixyra* (now *Gynandriris*) and *Dietes*, both now recognised as separate genera and treated as such by the present author. The diploid number of 20 and the much ramified habit of *Dietes* together with its rhizomatous rootstock suggest a primitive position with regard to *Moraea* where the rootstock is always a single internode corm.

Gynandriris has a cormous rootstock and a moderately branched stem. It differs from *Moraea* only in its ovary which is prolonged into a sterile upper portion or beak. Apart from this the group seems allied to the *Subracemosae* where a similar karyotype occurs.

Another species which appears misplaced in Baker's system is *M. polystachya*, referred by Baker to the *Corymbosae*. Morphologically, it is unlike most of that group for it is only little branched. As indicated by its karyotype, this vegetative habit belongs better in the *Subracemosae* where the branching is limited and a diploid number of 12 is found.

Baker's section *Monocephalae* appears to be an artificial grouping for two quite different karyotypes occur here, although morphologically the species are similar in being unbranched with a terminal inflorescence and having only a single leaf. This vegetative type may have evolved independently in the groups with 20 and 12 somatic chromosomes. There are, however, other features common to the two groups, and the most obvious of these being the nature of the seeds, which, in contrast to the round or angled seeds in the rest of the genus, are flat, disc-shaped structures with a rather spongy testa making them very light and easily distributed by the wind. The seed structure is not known in all species and the taxonomic significance of the distinctive seed needs further study. At present, however, it supports the contention that the *Monocephalae* are a natural group despite the great karyotypic variation found here.

Moraea lurida, also included by Baker in the *Monocephalae*, is clearly misplaced. It is sometimes branched and has a karyotype like that of the *Subracemosae* and *Vieusseuxia*. In the present author's opinion it is perhaps best placed in the latter group because, although the inner perianth segments are not tricuspidate or as small as in most members of the subgenus, the outer segments are the same shape, namely oval and not lanceolate. Its karyotype is perhaps closest to that of *M. bellendenii*, a member of the subgenus *Vieusseuxia*.

The origin and evolution of *Moraea*.

As postulated in the section on *Dietes*, the ancestor of the genus *Moraea* is suggested to be a plant with a much branched stem and many basal leaves. The species most resembling this are *M. odorata* and *M. ramosissima* both of which have a diploid number of 20 and which can also be regarded as having the least specialised karyotype in the genus. *Dietes*, the genus believed to be the ancestor of both *Moraea* and the related genus *Iris* also has a basic number of 10 with several species having 20 somatic chromosomes and a karyotype resembling that of *M. ramosissima*.

The differences between *Dietes* and *Moraea* have been mentioned already but can be mentioned again. The rootstock is a single internode corm in *Moraea* and a creeping rhizome in *Dietes*; *Moraea* has bifacial leaves with an equitant tip while *Dietes* has equitant leaves. Though their flowers are similar in structure and have petaloid styles with bifid crests, the filaments of the stamens are usually connate in *Moraea* and free in *Dietes* (fig. 5: A, B, C).

Within *Moraea* there is very little variation in the flower structure and this is not a very useful criterion in evaluating the evolution of the group. The subgenus *Vieusseuxia* is the exception, for here several species have very short style crests, and the other species have reduced tricuspidate inner perianth segments.

The greatest variation in morphology is in the vegetative habit. As observed by Baker and confirmed by the present study there seems to be a strong correlation between the evolution of the group and a reduction in complexity of the plant body. In some cases the reduction in branching and number of leaves has been accompanied by a change in the number of chromosomes and in other cases not, but a specialisation in karyotype leading to asymmetry is repeatedly observed.

The following phylogenetic scheme is proposed for the genus. There were presumably two main lines of evolution leading from the putatively primitive much ramified type; one leading to less branched species but still with several leaves and here, the diploid number of 20 was maintained. The end of this line is the *M. ciliata* group (*Acaules*) with several leaves and no visible aerial stem. Another line leading from the basic stock is the *M. angusta* group (*Mono-*

cephalae). Here both branching and leaf number is reduced and the seeds are flattened. In this line aneuploid reduction from 20 to 12 has presumably occurred.

Another trend, also leading to less branched species with fewer or a single leaf, was presumably accompanied by aneuploid reduction leading ultimately to the diploid number of 12. *M. papilionacea* with a somatic number of 18 is probably a link in this line. This evolutionary line (*Subracemosae*) is distinct from the *Monocephalae* in that branching is not quite lost and the seeds are angled. This line may have led to the subgenus *Vieusseuxia* with its specialised flowers and the genus *Gynandriris* where the ovary is modified to form a beak. These two groups are believed to have evolved independently from the *Subracemosae*, the least specialised group in this line of evolution.

c. The genus ***Gynandriris***

$2n = 12, 24.$

Gynandriris consists of about ten South African and one Mediterranean species. The species are herbaceous, corm bearing, and differ from *Moraea* only in having the ovary extended into a long sterile tube-like beak. The two species studied by the present author, *G. setifolia* and *G. torta*, both Cape species, have a diploid number of 12 (Table 5).

The karyotypes of these two species are similar and distinctive in having a rather large satellite on a pair of shorter chromosomes. Another similarity is the possession by both of an almost metacentric long chromosome (fig. 11: D, E).

The only species previously examined is *Gynandriris sisyrinchium* (as *Iris sisyrinchium*) the Mediterranean species, found by Simonet (1932) to have a somatic number of 24. In the light of the present study, this would appear to be a polyploid species. Simonet's description and illustration of the karyotype strongly supports this, as *G. sisyrinchium* has 4 long metacentric chromosomes and the 4 shortest have rather large satellites. This is remarkably like the karyotypes of both South African species studied and supports the inclusion of the Mediterranean species in this predominantly southern African genus.

Gynandriris is believed to be very closely allied to *Moraea*, in which it has frequently been included, and shares with it the very many features including the characteristic corm tunics. The difference between the genera is that *Gynandriris* has a pseudo-perianth tube formed by a sterile elongation of the ovary. This feature is unusual and can be regarded as a specialisation of the normal ovary occurring in *Moraea*. *Moraea* is a southern African genus and does not extend far beyond central Africa. *Gynandriris* shares this distribution except for *G. sisyrinchium* which extends to the Mediterranean area and eastwards into Asia as far as Afghanistan. The cytology confirms the suggested relationship between *Moraea* and *Gynandriris* and the karyotype of the latter is most similar to species of *Moraea* placed in the section *Subracemosae*.

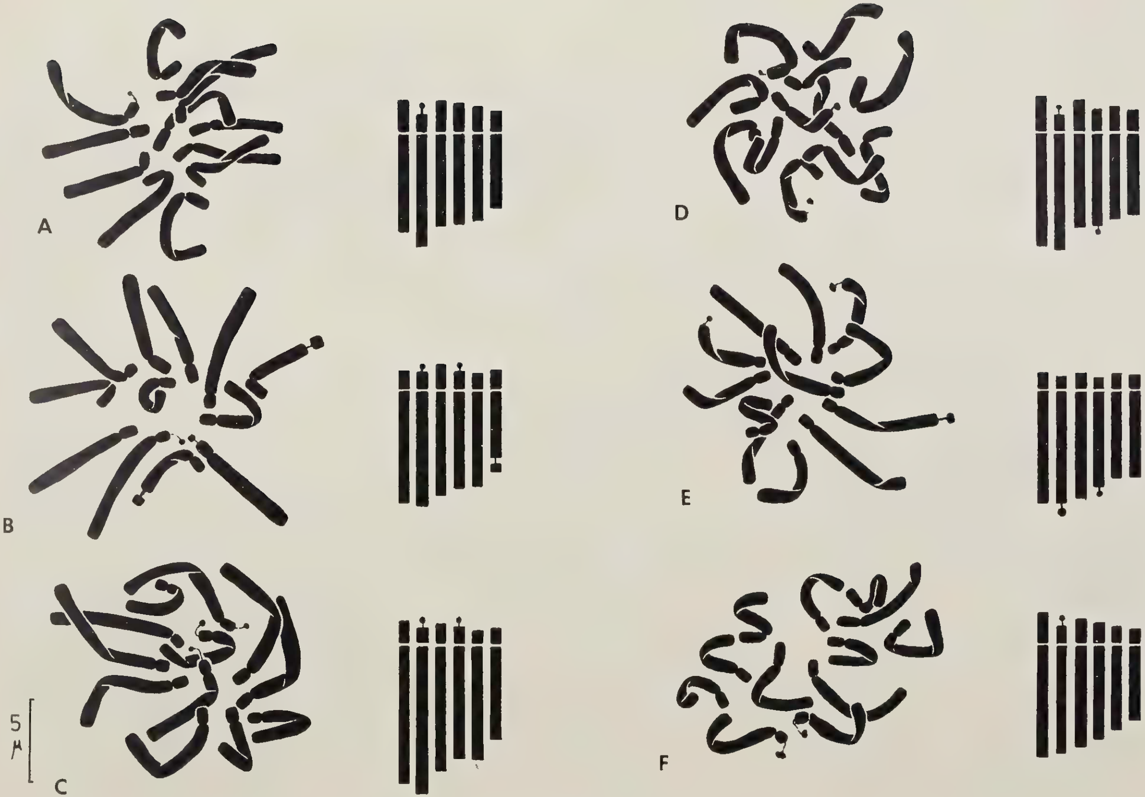

FIG. 12.
Karyotypes and idiograms of *Homeria*. A. *Homeria pura;* B. *H. ochroleuca;* C. *H. miniata;* D. *H. glauca;* E. *H. tricolor;* F. *H. papillosa.*

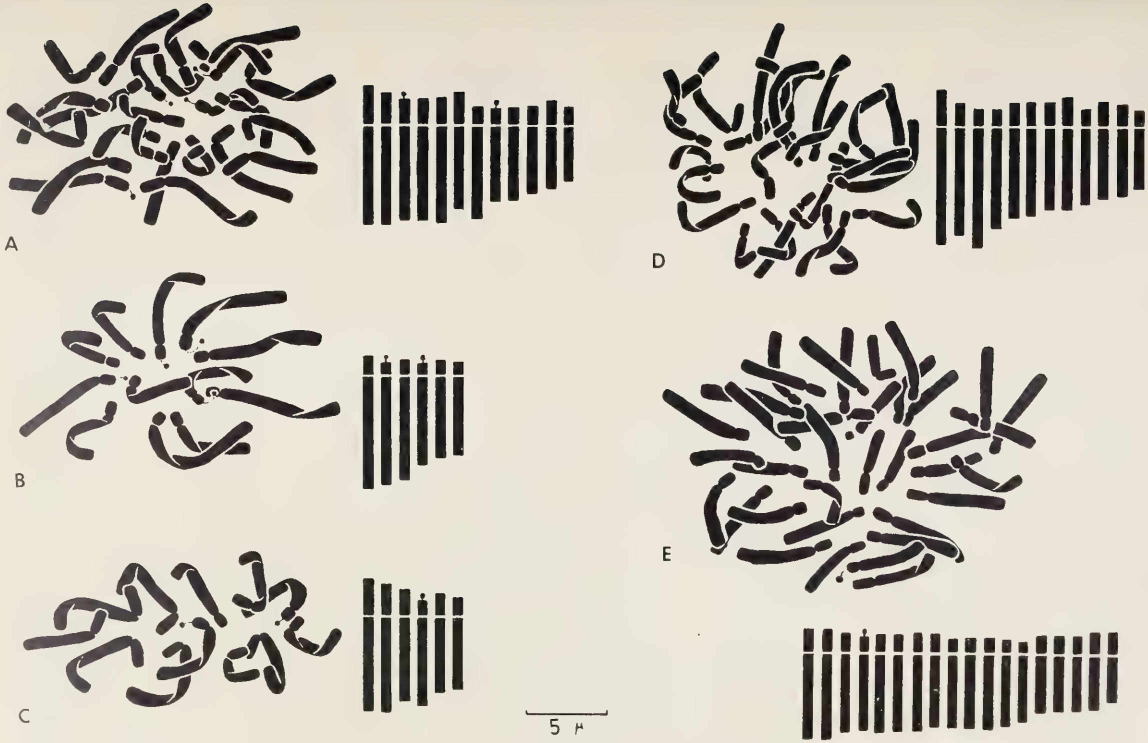

Fig. 13.
Karyotypes and idiograms of *Homeria*. A. *Homeria pallida*; B. *H. maculata*; C. *H. lilacina*; D. *H. breyniana*; E. *H. breyniana* var. *aurantiaca*.

In a recent classification of *Iris* (Lawrence 1953), *Gynandriris sisyrinchium* was incorporated in *Iris* again, in a section of its own. This treatment ignores the African genera *Dietes* and *Moraea* which are also closely related to *Iris*. On the criteria Lawrence uses to transfer *Gynandriris*, *Moraea* and *Dietes* must also be included in *Iris*. This would clearly be an impractical step. The alternate is to continue to recognise both *Moraea* and *Dietes* and in doing so, *Gynandriris* must be maintained as distinct, or be included in *Moraea*, the genus to which it is most closely allied according to both cytological and morphological evidence.

d. The genus ***Homeria***

$2n = 12, 24, 36.$

Homeria is a fairly large genus of small herbaceous plants found throughout southern Africa. It is allied to *Moraea*, having a similar corm and a bifacial leaf. The difference between the two is that *Homeria* lacks the petaloid style with the usual long crests. The perianth segments are subequal, spreading and rarely unguiculate as in *Moraea*.

Ten species and a variety of the approximately 30 species were studied here. Eight of these have a diploid number of 12 (Table 7). Two species have somatic numbers of 24 and the variety of one has 36 chromosomes. The chromosomes are large and are mostly acrocentric. Each species has its own distinctive though similar karyotype as can be seen from the illustrations (fig. 12, 13). Most species have two pairs of chromosomes bearing a satellite but there are several exceptions. One satellite is usually located on the end of the short arm of the second chromosome. In some species the satellite is on the end of the long arm of a chromosome as in *H. tricolor*. The position of the satellites is a very distinctive feature of the karyotype and together with the relative lengths of the arms of the chromosomes, gives each species its distinctive karyotype.

The polyploid species proved a little difficult to analyse and here the satellites were not seen clearly. Absence of satellites in the idiograms of polyploids probably does not mean that these plants lacked these structures but that they were more difficult to observe.

The first cytological report on *Homeria* was that of Brittingham (1934) who found a somatic number of 36 in *H. elegans*. Sakai (1952) reported a somatic number of 24 in *H. breyniana* (as *H. collina*) and a number of 36 in an unidentified species. The count for *H. breyniana* is confirmed by the present author although the karyotype illustrated by Sakai differs somewhat from that found here. Sakai found that the longest chromosome was metacentric while in the plants studied by the present author the longest chromosome is rather acrocentric. Brittingham's report for *H. elegans* is, however, not supported. It is possible that an error occurred in the identification of his plant.

Several separate populations of *H. breyniana* were examined by the present author and all proved to have 24 chromosomes. A study of meiosis in this species showed that this process was quite normal. *H. breyniana* thus appears to be an allotetraploid species. The variety of this tetraploid species proved to have 36 chromosomes. Here meiosis was also normal and var. *aurantiaca* appears to be a normal hexaploid form. The present author's opinion is that it should be regarded as a distinct species for it grows and flowers in the same localities as *H. breyniana* var. *breyniana* and is clearly reproductively isolated by virtue of its difference in ploidy.

TABLE 7

Chromosome numbers in *Homeria*, *Hexaglottis*, *Galaxia* and *Ferraria*

Species	Diploid No.	Collection Data or Reference
HOMERIA Vent.		
H. pura N. E. Br.	12	Bryanston, Johannesburg, Tvl. *Goldblatt 34* (J)
H. ochroleuca Salisb.	12	Kirstenbosch, C.P. *Goldblatt 510*
H. miniata (Andr.) Sweet . .	12	Garies, C.P. *Goldblatt 119* (J)
H. glauca (Wood & Evans) N. E. Br.	12	Tvl. (ex hort) *Goldblatt 95* (J)
H. tricolor L. Bol.	12	Touws River, C.P. *Goldblatt 65* (J)
H. papillosa L. Bol.	12	Van Rhyns Pass, C.P. *Goldblatt 131* (J)
H. pallida Bak.	24	Sterkstroom, C.P. *Goldblatt 67* (J)
H. elegans (Jacq.) Sweet . . .	12	Caledon, C.P. (ex. hort) *Goldblatt 51* (J)
	24	(Brittingham 1934)
H. lilacina L. Bol.	12	Robertson, C.P. *Goldblatt 141* (J)
H. breyniana (L.) Lewis . . .	24	Fish Hoek, C.P. *Goldblatt 507*
(as H. collina)	24	(Sakai 1952)
H. breyniana var. aurantiaca (Sweet) Bak	36	Cape Town, C.P. *Goldblatt 133* (J)
H. sp.	36	(Sakai 1952)
HEXAGLOTTIS Vent.		
H. flexuosa (L.f.) Sweet . . .	12	Loeriesfontein, C.P. *Goldblatt 108* (J)
H. virgata (Jacq.) Sweet . . .	10	Signal Hill, Cape Town, C.P. *Goldblatt 71* (J)
GALAXIA Thunb.		
G. citrina Lewis	16	Cold Bokkeveld, C.P. *Goldblatt 318*
G. fugacissima (L.f.) Druce . .	16	Rondebosch, C.P. *Goldblatt 321.*
G. c.f versicolor Lewis (flowers not seen)	16	Nieuwoudtville, C.P. *Goldblatt 311*
G. ovata Thunb.	32	Hout Bay, C.P. *Goldblatt 316.*
FERRARIA L.		
F. longa Barnes	20	Botterkloof, C.P. *Goldblatt 432*
F. undulata L.	60	Cape Town, C.P. *Goldblatt 47* (J) (ex hort)
F. cf. framesii L. Bol (flowers not seen)	20	Caledon area, C.P. (ex hort) *Goldblatt 511*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P., Transvaal—Tvl. Specimens are housed in the Bolus Herbarium unless stated to the contrary.

Homeria pallida, the other polyploid, is a widespread species occurring in the summer rainfall area of the Karoo. *H. pura* ($2n = 12$) is considered to be synonymous with *H. pallida* by some authorities. It has a limited distribution in the Transvaal highveld and differs morphologically to some extent. The present investigation shows that the two differ in chromosome number and this, together with the morphological difference is evidence that the two should be recognised as distinct species.

Homeria appears to be a distinct and natural genus but examination reveals that it and *Moraea* differ in few aspects. In the majority of species of *Moraea* there is a marked difference between the perianth segments, for the inner are usually small and erect and the outer large and spreading. There are, however, several species which have quite large and spreading inner segments, e.g. *M. lurida* and *M. insolens*. Species with this type of perianth differ from *Homeria* only in the nature of the style which can, in both, be petaloid and bifid. In *Moraea*, however, the bifid apex or crests, extending above the stigmatic lobe, are longer than in *Homeria* where the crests are absent or shorter than the width of the stigma. Occasionally, however, the crests are fairly short in some species of *Moraea*, e.g. *M. gigandra* and here the style resembles that of *Homeria* (fig. 5: D).

Thus *Moraea* and *Homeria* seem to merge together rather indistinguishably and it is occasionally difficult to assign a species to one or the other genus. The two genera are, however, probably distinct in spite of their occasional similarities and *Homeria* must be retained if only on the grounds of convenience. The nature of the style branches remains the only good character for distinguishing these genera. In *Homeria* they are simpler and it is sometimes possible to see how this rather unusual organ is constructed (fig. 5: E, F). The crests appear to be extensions of the margins lateral to the stigmatic surface and have curved upwards to form a small erect crest. The recurved margins meet above the middle of the stigma but are fused only at the base. This structure can be seen in some species of *Homeria* (e.g. *H. marlothii*), while in *Moraea* the crests do not appear to be part of the stigma for they are quite separate from its edge (fig. 5: B, C). The style crests appear to be the continuation of the style branches and the stigmatic lobes lie on the abaxial surface of the style branch. The stigma thus appears in many *Moraeas* to be an independent extension of the lower surface of the style. This in effect means that the crests have fused with the back of the stigma. This distinction between two genera is in practice often rather difficult to see, but may help in critical species.

The phylogeny of *Homeria* is problematical. The genus can be considered as either advanced in relation to *Moraea* or primitive. If it is primitive then the seemingly less complex style and the simpler flower are easy to understand, for both these structures can be regarded as being more specialised in *Moraea.*

This hypothesis has rather disturbing consequences because *Dietes*, believed to be the ancestor of *Iris* and *Moraea*, has a rhizome and several other primtive features, but it has a petaloid style like that of *Moraea*. Thus if *Homeria* is considered to be primitive, but leading to *Moraea*, it must also be ancestral to *Dietes*. This is clearly not the case for *Homeria* has a specialised bifacial leaf and a corm and has connate stamens also found in *Moraea* but not *Dietes*.

An alternative hypothesis, that *Homeria* is phylogenetically advanced over *Moraea*, appears more tenable. In this case the bifacial leaf, connate stamens and characteristic corm found in both genera indicate close relationship and the less complex flower and style must be explained as reduction of an already modified structure. This means that those species of *Homeria* lacking style crests are the most advanced in this genus. This theory is attractive for it helps to explain the nature of the style of *Galaxia*, an obviously reduced and modified genus which has many of the features of *Homeria* but its style is reduced to a column with simple stigmatic lobes at its apex.

Other theories of the phylogeny of *Homeria* can also be suggested but apart from the previous one, only that of parallel evolution can be accepted. This would be remarkable, if correct, for the evolution of an identical corm and other vegetative modifications such as the bifacial leaf and reduction of branching would have had to occur together with the development of connate stamens and a crested sub-petaloid style.

From the cytological point of view the theory that *Homeria* is derived by simplification from *Moraea* is most acceptable. Species of *Moraea* most resembling *Homeria* in vegetative structure are those which have a basic chromosome number of 6, the same as is found in *Homeria*. These species of *Moraea* appear the most specialised in the genus, for they usually have a single leaf and few branches and their karyotype does to some extent resemble that of *Homeria*.

e. The genus ***Galaxia***

$2n = 16.$

Galaxia is a small genus of reduced plants which lack an aerial stem. The rootstock is a corm much like that found in *Moraea* and the leaves are bifacial. The scape is very reduced so that the inflorescences are subterranean and the fugaceous flowers are raised above the ground by the long perianth tube. The genus is in a state of considerable taxonomic confusion for there appear to be few characters on which to distinguish species. Although there are a large number of names in the literature, only five species seem to be recognised today. It is believed that the cytology of four distinct species was studied by the present author but owing to the difficulty with identification this may later require correction.

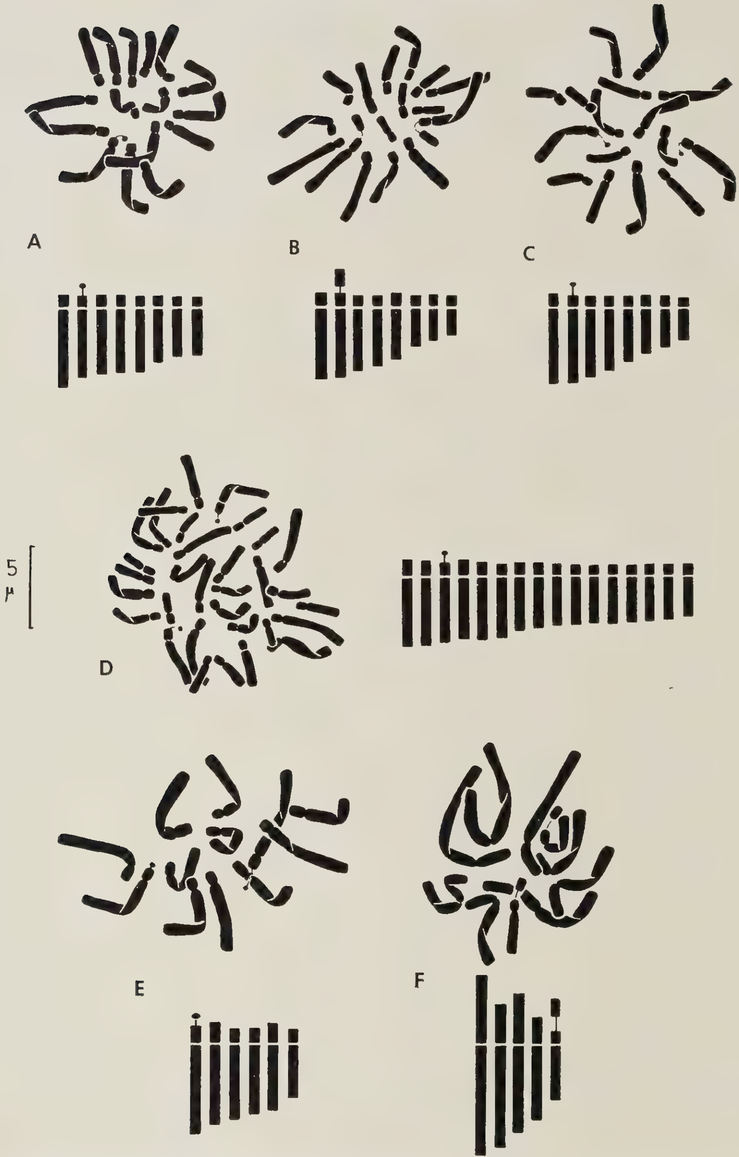

Fig. 14.
Karyotypes and idiograms of *Galaxia* and *Hexaglottis*. A. *Galaxia citrina;* B. *G. fugacissima* C. *G. cf. versicolor;* D. *G. ovata;* E. *Hexaglottis lewisae;* F. *H. virgata.*

Three species were found to have a diploid number of 16 while a plant from the Cape Peninsula, referred to *G. ovata*, proved to be polyploid with 32 somatic chromosomes (Table 7). The chromosomes are acrocentric and the second longest pair bears a satellite, which in *G. fugacissima*, is particularly large (fig. 14: A, B, C, D). The cytology of this genus has not previously been studied so the counts in this work are new records. There is a strong indication that the basic number for *Galaxia* is 8.

Galaxia is modified in a manner similar to *Syringodea* and *Crocus*, as the aerial stem is reduced and does not extend above ground level and the flowers are raised above the ground by a long perianth tube. The genus was originally classified with *Romulea*, *Syringodea* and *Crocus* in a single group but as already mentioned, Lewis (1954) showed that *Galaxia* really belonged to the *Irideae* and the other three to the *Ixieae*. This decision of Lewis has been validated by cytological study for it has the long chromosomes characteristic of this group.

Lewis believed that the genus was allied to *Homeria* for it has the type of corm found in this genus and its allies. Another feature it shares with this group is the position of the stamens which are opposite the stigmas. *Galaxia* is clearly modified for it is reduced in size, has broad bifacial leaves and the flowers are solitary as opposed to cymes in the other genera. The perianth tube also seems an advanced feature for it is not characteristic of *Homeria* and its allies. The style and stigma are simpler than in the other members of the *Irideae* and consist of a column with three expanded stigmatic lobes at the apex. If Lewis' suggestion is correct that *Galaxia* is derived from *Homeria*, which usually has a branched petaloid style, the condition in *Galaxia* has been reached by reduction and fusion of the style branches (fig. 5).

Galaxia is placed closest to *Homeria* in the *Irideae* because, like *Homeria*, it has fairly simple flowers with subequal and spreading perianth segments. The basic number in *Homeria* is 6 and that in *Galaxia* 8, which could have been derived from 6 by increasing aneuploidy. This theory of the origin of *Galaxia* has alternatives for it could easily have been derived from *Moraea* which has a more specialised flower, by reduction and simplification. Haploid numbers of 12 down to 6 occur in *Moraea* and there are reduced species in this genus though these still retain the flower typical of *Moraea*.

f. The genus ***Hexaglottis***

$2n = 12, 10.$

Hexaglottis is a small genus allied to *Moraea* and *Homeria*. It has the corm and bifacial leaf typical of this group. The very fugaceous flowers are actinomorphic with subequal, spreading segments. The genus is distinguished by its deeply divided style branches, which divide into two slender arms, at the ends of which are located the stigmatic surfaces.

Two of the four species in this genus were studied, both for the first time (Table 7). The diploid number for *H. flexuosa* is 12 and for *H. virgata*, 10. The chromosomes are long and the karyotype of *H. flexuosa* resembles that of *Homeria* in consisting of acrocentric chromosomes with a satellite on one of the longer pairs (fig. 14: E, F).

The karyotype of *H. virgata* is rather different for the chromosomes tend to be sub-metacentric and the longest and third chromosomes are almost metacentric. The shortest of the 5 pairs of chromosomes has an unusually large satellite. This karyotype could be described as symmetric in the terminology of Stebbins (1950) who shows that it is frequently more primitive than the asymmetric karyotype like that of *H. flexuosa*, although not necessarily so when aneuploid reduction takes place (Jones 1970).

According to Lewis (1954), *Hexaglottis* is most closely related to *Homeria* though she considered it in some respects less specialised, e.g. the style branches are slender in *Hexaglottis* but large and sub-petaloid in some of Homeria (fig. 5). The similarity of the karyotypes of species of *Homeria* to *Hexaglottis flexuosa* tends to confirm Lewis' opinion. *H. virgata* is a more specialised species of *Hexaglottis* for it is the only one possessing a perianth tube and it also has sessile flowers, completely lacking the short pedicels found in other species. Thus it is unlikely that the most specialised species of *Hexaglottis* should have a primitive karyotype. This is more likely a case of aneuploid reduction accompanied by a redistribution of chromosome material which has resulted in the unusual karyotype of *H. virgata*. This hypothesis could possibly be tested if this species could be crossed with another *Hexaglottis*. This would be a little difficult for the flowers last for only a few hours and wilt rapidly, but the cross could be performed if the species were cultivated together under laboratory conditions.

The evolution and significance of the style in *Hexaglottis* is problematic. It is this character which distinguishes *Hexaglottis* from *Homeria*. The three style branches are opposite the stamens but are forked almost to the base so that they extend on either side of the anther (fig. I, J). Thus there appear to be six style branches, two between each anther. In *Homeria* the style branches are only slightly forked above each of the three stigmas but *Hexaglottis* has a stigmatic area at the tip of each style branch.

If, as already discussed, the almost petaloid style of Homeria is reduced from that of *Moraea*, *Hexaglottis* can be interpreted as having a further reduced style where the petaloid nature has been lost completely. This interpretation implies that *Hexaglottis* is not more primitive than *Homeria*, as Lewis suggested, but rather derived from it. Unfortunately, there do not appear to be any other features in the two genera which differ sufficiently to throw light on the relationship between them.

g. The genus ***Ferraria***

$2n = 20, 60.$

Ferraria is a comparatively small genus of perhaps twelve species. It is found from tropical Africa to the Cape Province where most species occur. These species were studied here, all from the south western Cape Province (Table 7). *F. longa* and *F. framesii* have a diploid number of 20, while *F. undulata* was found to be hexaploid with a somatic number of 60. Three geographically separate populations of this species were examined and all exhibited the same level of polyploidy.

There has been no previous report on the cytology of this genus. It appears from the present study that the basic number for the genus is 10. The chromosomes are long but the karyotype is distinctive in having a large number of comparatively short chromosomes (fig. 15).

Ferraria belongs to the *Irideae* and has the elaborate style with stamens opposite the branches, found in many genera of the group. It is unusual in having a feathery dissected petaloid apex of the style above the stigma. The perianth segments are subequal and spreading with the distal portions reflexed downwards and the margins of the segments are crisped. Most species are unpleasantly scented, and have rather dull markings characteristically in the form of spots. The flower thus appears to be very specialised and it is believed to be modified for pollination by flies.

The vegetative parts of the plant are less modified; the rootstock is a type of corm; the leaves are equitant, and the plant much ramified. The corm is peculiar for it has very fine tunics which soon disintegrate. Because these fine tunics were often overlooked the rootstock was often regarded as a tuber. The corms are persistent and plants often have the corms of several past seasons attached in a line to the growing portion. The corm itself is of the single internode type found in other African *Irideae* but it is probably less specialised than these in being long lived and having rather poorly developed tunics.

Ferraria has in the past been regarded as more closely allied to the South American genera of the *Irideae*, e.g. *Tigridia*, than to any South African group. *Tigridia* has a flower superficially resembling that of *Ferraria* but the style and stigma are not petaloid or dissected and the rootstock is a bulb, not a corm. Cytologically the two genera differ, for although the chromosomes are relatively large, the diploid number in *Tigridia* and in closely allied genera has been shown to be consistently 28 (Molseed 1970). The resemblance between these two genera may thus be entirely fortuitous.

The present author prefers to regard *Ferraria* as a derivative of the South African *Irideae* which diverged early from the line leading to *Moraea* but after the single internode of the group corm had been evolved.

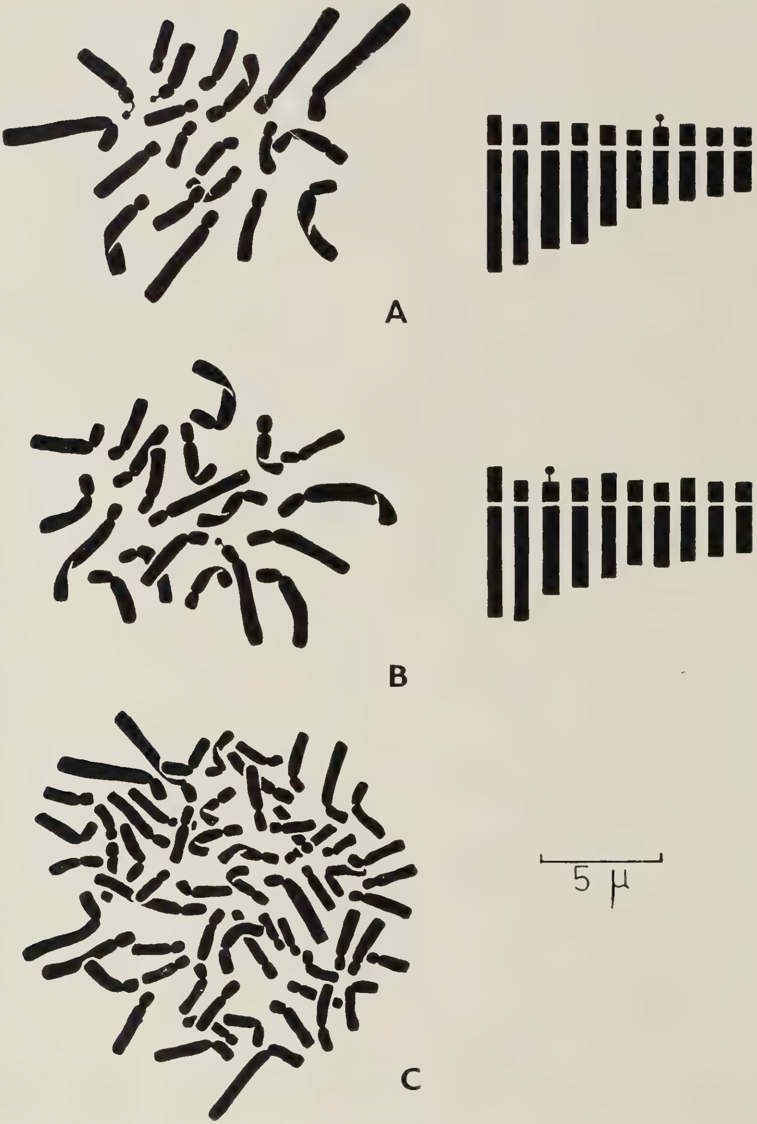

Fig. 15.
Karyotypes and idiograms of *Ferraria*. A. *Ferraria longa;* B. *F. cf. framesii;* C. *F. undulata.*

h. Conclusions

The subdivisions of the tribe *Irideae*

It is proposed to recognise three subtribes in the southern African members of the Irideae. *Dietes*, *Moraea* and *Gynandriris* together with *Iris* appear to comprise a single natural unit, the subtribe *Iridineae*. Although some variation does occur in several vegetative characters, the petaloid nature of the style branches and the unequal perianth segments are common to all representatives. *Homeria*, *Hexaglottis* and *Galaxia* probably form a second natural group for which the name *Homeriineae* is suggested. In this group the style is not petaloid and the perianth segments are subequal and spreading. *Ferraria*, with its equitant leaves and persistent corm with membranous tunics in contrast to the usually bifacial leaves and short-lived corm covered by fibrous tunics, does not fit in either of the above groups and must be placed in a third subtribe *Ferrariineae*. Whether this last genus is really allied to the new world genera as is often suggested, remains unknown at present and these must be examined more critically both morphologically and cytologically.

4.4. Tribe 3. IXIEAE.

Members of this tribe are mainly African in distribution. It comprises about thirty-three genera only three of which extend into Europe and Asia. Generally the group is distinguished by a cormous rootstock, equitant leaves, though these are often modified, and a spicate inflorescence of non-fugaceous flowers. Considerable specialisation of various structures has occurred in some genera, resulting in reduced plants such as *Crocus* which appear an exception to the above description.

CYTOLOGY, POSSIBLE PHYLOGENY AND CLASSIFICATION INTO SUBTRIBES

a. Subtribe ***Watsoniineae***

Watsonia, Pillansia, Thereianthus & Micranthus

This group is distinguished by the tough fibrous corm tunics, very fibrous, ensiform leaves and, with the exception of *Pillansia*, a spicate inflorescence with the flowers arranged distichously. The flowers have a well-developed perianth tube and forked style branches.

WATSONIA

2n = 18, 27.

Watsonia is a large genus of typically montane species occurring in southern Africa and Madagascar. When found in low lying areas the plants are associated with damp conditions. The species vary in size, many being the largest plants in the tribe, and reaching to about 1,5 m. The flowers are large and brightly coloured, the seeds are distinct from the other genera in this group in being winged and the leaves always fairly broad and sword shaped.

TABLE 8

Chromosome numbers in *Watsonia*, *Pillansia*, *Thereianthus* and *Micranthus*.

Species	Diploid No.	Collection Data or Reference
WATSONIA Miller		
W. brevifolia Ker	18	Napier, C.P. *Goldblatt 337*
W. ardernei Sanders	18	Kirstenbosch (ex hort) *Goldblatt 57* (J)
	16 + 2	(Riley 1962)
W. pyramidata (Andr.) Stapf.	18	Stettyns Kloof, C.P. *Goldblatt 468*
W. beatricis Mathews & L. Bol.	18	Kirstenbosch, C.P. (ex hort) *Goldblatt 58* (J)
W. aletroides Ker	18	Caledon, C.P. *Goldblatt 38* (J)
W. fulgens (Andr.) L. Bol.	18	Skurweberg, Ceres, C.P. *Goldblatt 482*
W. humilis Miller	18	Table Mountain, C.P. *Goldblatt 405*
W. meriana Miller	18	Oudekraal, C.P. *Goldblatt 140* (J)
W. tabularis Mathews & L. Bol.	18	Cape Point Reserve, C.P. *Goldblatt 155* (J)
W. bulbillifera Mathews & L. Bol.	27	Kirstenbosch, C.P. (ex hort) *Goldblatt 53* (J)
W. vivipara Mathews & L. Bol.	18	Ceres, C.P. *Goldblatt 477*
W. angusta Ker.	18	Stettyns Kloof, C.P. *Goldblatt 476*
W. transvaalensis Bak.	18	Haenertsburg, Tvl. *Goldblatt 56* (J)
W. alpina Lewis	18	Graskop, Tvl. *Goldblatt 522* (J)
W. latifolia Oberm	18	Wakkerstroom, Tvl. *Goldblatt 76* (J)
W. galpinii L. Bol.	18	Eastern C.P. *Goldblatt 84* (J)
W. stenosiphon L. Bol.	18	Quoin Point, C.P. *Goldblatt 479*
W. marginata (L.f.) Ker.	18	Kirstenbosch, C.P. (ex hort) *Goldblatt 488*
W. fourcadei Mathews & L. Bol.	18	(Riley 1962)
W. sp. (as W. iridifolia)	18	(Sharma & Talukdar 1960)
	18	(Nakajima fide Darlington & Wylie 1955)
W. hort. var.	16	(Brittingham 1934)
PILLANSIA L. Bol.		
P. templemanii (Bak) L. Bol.	44	Rooi Els, C.P. *Goldblatt 471*
THEREIANTHUS Lewis		
T. bracteolatus (Lam) Lewis	20	Houw Hoek Pass, C.P. *Goldblatt 68* (J)
T. lapeirousioides (Bak.) Lewis	20	Bains Kloof, C.P. *Goldblatt 190*
MICRANTHUS Pers. ex. Eckl.		
M. plantagineus (Pers) Eckl.	20	Elgin, C.P. *Goldblatt 69* (J)
M. tubulosus (Burm.) N. E. Br.	20	Kirstenbosch, C.P. (Ex hort) *Goldblatt 489*
M. junceus (Bak.) N. E. Br.	20	Caledon, C.P. *Goldblatt 395*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P., Transvaal—Tvl. Specimens are housed in the Bolus Herbarium unless stated to the contrary.

Eighteen of the approximately seventy recognised species were studied, (Table 8) and all except one have a diploid number of 18 comparatively small chromosomes. The karyotype is very characteristic, consisting of 2 pairs of long chromosomes, measuring between 2 and 4μ, a pair of medium length of

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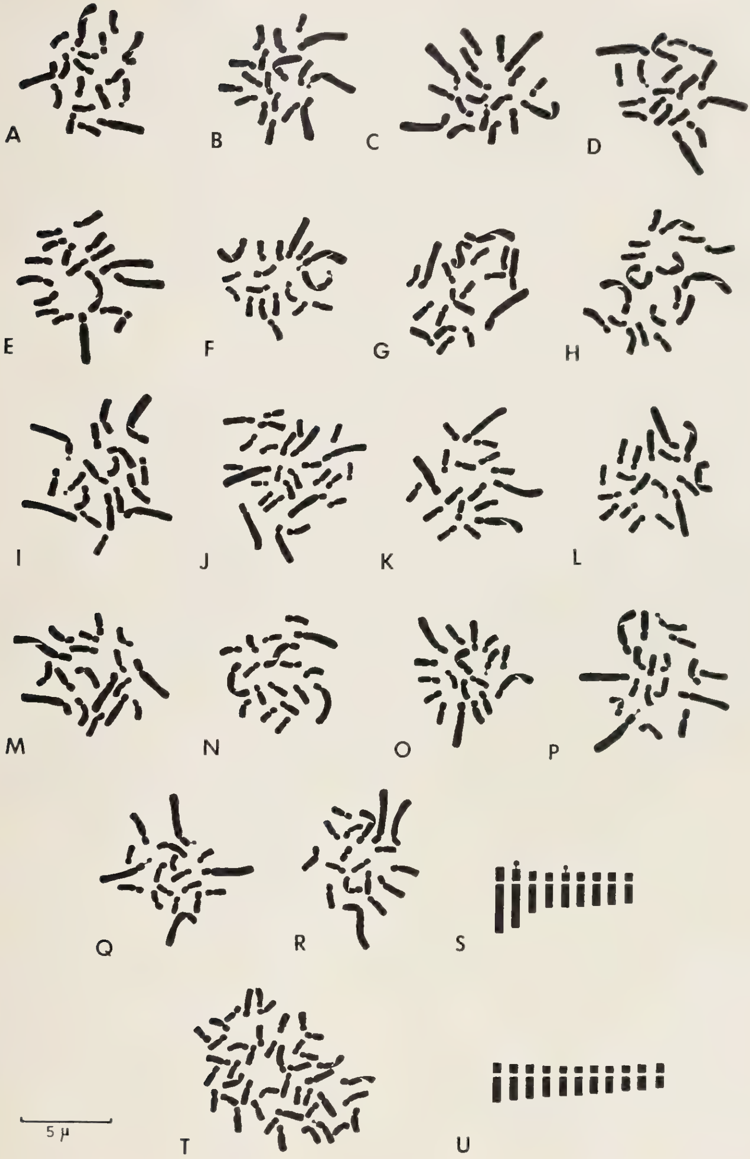
FIG. 16.

Karyotypes and idiograms of *Watsonia* and *Pillansia*. A. *Watsonia brevifolia;* B. *W. ardernei;* C. *W. pyramidata;* D. *W. beatricis;* E. *W. aletroides;* F. *W. fulgens;* G. *W. humilis;* H. *W. meriana;* I. *W. tabularis;* J. *bulbillifera;* K. *W. vivipara;* L. *W. angusta;* M. *W. transvaalensis;* N. *W. alpina;* O. *W. latifolia;* P. *W. galpinii;* Q. *W. stenosiphon;* R. *W. marginata;* S. Idiogram of *Watsonia;* T. *Pillansia templemanii;* U. Idiogram of *Pillansia.*


A
B
C
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5 μ

about 2,5μ and the remaining 6 pairs of short chromosomes of about 1,5μ long (fig. 16: A—S). The exception is *W. bulbillifera* which has 27 somatic chromosomes. This species is clearly triploid and as would be expected has 6 long, 3 medium and 18 short chromosomes.

The chromosomes are acrocentric and there appear to be satellites on two pairs of chromosomes. Although all the satellites are seldom seen, several metaphase plates exhibit a satellite on one of the long and one of the short chromosomes. This characteristic is believed to be constant though difficult to see and is represented in the idiogram of *W. pyramidata* shown here as representative of the genus.

Prior to this study, only four species of *Watsonia* had been described cytologically. Brittingham (1934) found a diploid number of 16 in an unidentified horticultural variety. Darlington & Wylie reported that Nakajima found a diploid number of 18 in *W. iridfolia* (a name used for many horticultural forms, but probably close to *W. meriana*). Sharma and Talukdar (1960) also found 2n = 18 for a form they referred to *W. iridifolia.* Riley found 2n = 18 in *W. fourcadei,* but in *W. ardernei* 2n = 16 plus two supernumaries. Present investigation of *W. ardernei* revealed that it does not differ from the other species of *Watsonia* but has 18 somatic chromosomes. Thus the supernumaries described by Riley for this species were probably a pair of small somatic chromosomes. Brittingham, who also found a diploid number of 16 may have been mistaken in his interpretation of the karyotype. His illustration shows 6 long chromosomes, 2 of which have marked medium constrictions, and these are probably really 2 small chromosomes lying very close together. If this interpretation is correct, Brittingham's work is in accord with the other chromosome studies in *Watsonia.*

Sharma and Talukdar described the karyotype of the species they studied as consisting of 4 long, 2 medium and 12 short chromosomes. Essentially the same results were obtained in the eighteen species studied by the present author. As altogether twenty of the seventy species of *Watsonia* have now been cytologically studied, it can be said with confidence that the basic number is 9 and the karyotype consists of 2 long pairs of chromosomes, one bearing a satellite, 1 medium pair and 6 short pairs, one of these also bearing a satellite.

The observation that *W. bulbillifera* has 27 chromosomes indicates that this species is triploid. An examination of pollen mother cells undergoing meiosis revealed the reduction division was totally abnormal and many trivalents and univalents occur. Though pollen is formed it is abnormal and there is an extraordinary variation in pollen grain size. The suggestion that this is a sterile triploid species is substantiated by the fact that it does not reproduce sexually but by means of cormlets which are produced in great numbers from all the nodes on the penduncle after flowering is over.

W. bulbillifera is closely related to *W. vivipara* which also produces large numbers of bulbils. In this case, however, the bulbils are produced while the plant is flowering. This latter species does reproduce sexually and produces viable seed. It has a wide distribution, occurring in the Warm Bokkeveld and the Montagu Karoo, while *W. bulbillifera* is restricted to the Cape Flats and Peninsula. *W. vivipara* is slightly smaller than *W. bulbillifera* in both flower size, height and leaf width but the differences are only quantitative, and to be expected between diploid and polyploid. It is likely that *W. bulbillifera* is only a race differing cytologically from its parent species, *W. vivipara.* The possibility of allopolyploidy cannot, however, be excluded, which would imply a hybrid origin with *W. vivipara* as one of the parents.

PILLANSIA

2n = 44.

Pillansia is a monotypic genus and is restricted to the coastal portion of the Caledon area of the western Cape. Vegetatively, the plant resembles *Watsonia,* but the inflorescence is branched and panicle-like and the corms are persistent. *Pillansia templemanii* has a diploid number of 44. The chromosomes are all acrocentric and small (fig. 16: T), ranging from 1 to 2μ in length. Careful examination reveals that there are 4 pairs of somewhat longer chromosomes which may be described as medium in length. As this species is believed to be a polyploid (as will be discussed later) the idiogram is shown comprising only eleven chromosomes (fig. 16: U).

This is the first chromosome count for this species. The somatic number of 44 is unusually high and indicates the possibility of polyploidy. To exclude the possibility of an isolated polyploid population having been studied, a geographically separate population was also examined. Here also the somatic number was found to be 44. A study of meiosis in pollen mother cells revealed 22 bivalents and meiosis appeared to be quite normal, thus indicating autopolyploidy as unlikely, although recent work has shown that bivalents only, may occur in known autopolyploids.

Pillansia templemanii is an unusual species which has a very limited distribution. It was believed by Lewis (1954) to be the ancestor of *Watsonia* and its allies because it has many of the watsonioid characteristics, e.g. the tough corm tunics, broad fibrous leaves and bifid stigmas. Its more primitive characteristics are its regular flowers, short perianth tube and branching paniculate inflorescence. It is thus believed to be a relict polyploid belonging to the group of plants which gave rise to the more specialised *Watsonia* and allies.

MICRANTHUS

2n = 20.

Micranthus is a small genus found in the south western Cape Province. The plants are small and flower in early summer. The resemblance to *Watsonia* is strong, but the flowers are very small and the leaves narrow to terete.

The three species in the genus were all found to have a diploid number of 20 (Table 8). All have a similar karyotype which consists of a single pair of long chromosomes of about 3μ in length, a pair of medium chromosomes measuring 2μ and 8 pairs of small chromosomes measuring less than $1{,}5\mu$ (fig. 17: A, B, C). The chromosomes are acrocentric and the long pair bears a satellite. The idiogram shown here is based on all three karyotypes (fig. 17: D). The chromosome counts are new records for the genus which clearly has a basic number of 10.

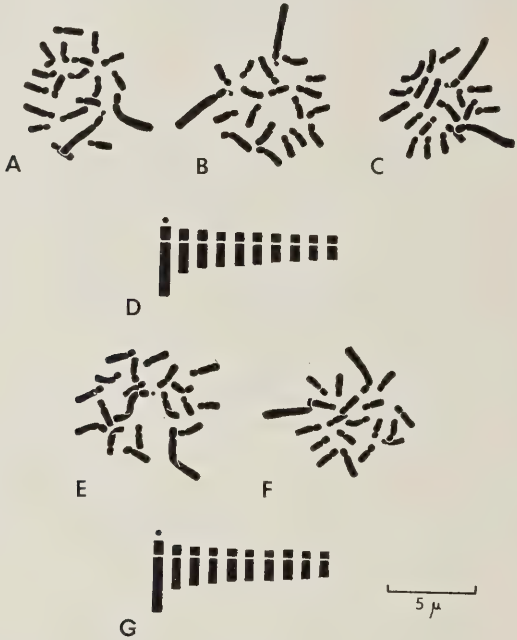


Fig. 17.
Karyotypes of *Micranthus* and *Thereianthus*. A. *Micranthus plantagineus;* B. *M. tubulosus;* C. *M. junceus;* D. Idiogram of *Micranthus;* E. *Thereianthus bracteolatus;* F. *T. lapeirousioides;* G. Idiogram of *Thereianthus*.

THEREIANTHUS

2n = 20.

Thereianthus is a small genus closely allied to *Watsonia*. The plants are small, usually purple flowered and bloom in summer. The narrow to terete, mucronate leaves are like those of *Micranthus*.

Two of the eight species, *Thereianthus bracteolaris* and *T. lapeirousioides* were studied by the present author. In both the diploid number is 20 (fig. 17: E, F) and the karyotypes similar to those of *Micranthus*. Again a general idiogram is illustrated, based on both species studied (fig. 17: G). The resemblance to *Micranthus* is quite unmistakable.

The two counts in this work are new records for the genus. *Thereianthus* was established by Lewis (1941) as a segregate of *Watsonia* and consisted of the smaller flowered summer blooming species then included in *Watsonia*. The difference in the karyotype is added confirmation of the validity of Lewis' treatment.

Although only two of the six species in the genus were studied, it is assumed that these are representative and that the basic number for the genus is 10. A comparison of the idiograms of *Micranthus* and *Thereianthus* shows the remarkable similarity of their karyotypes. It is clear that although *Thereianthus* was comparatively recently recognised as a segregate of *Watsonia* it is in fact more closely related to *Micranthus*.

Although the karyotypes are so similar and the two genera have several morphological features in common, the differences in the inflorescence and flower structure indicate that they should continue to be considered separate entities. While their corms are very similar and the mucronate leaves of both are unique in the family, their flowers and inflorescences are characteristic.

Thereianthus has a few quite large, either actinomorphic or subzygomorphic, flowers with a straight perianth tube, while *Micranthus* has many small zygomorphic flowers with a curved perianth tube.

Evolution of *Watsonia* and its allies

Pillansia is believed to be the ancestor of *Watsonia* and its allies though as mentioned, *P. templemanii* appears to be a relict polyploid. If this assumption is correct, the evolution of the group has been accompanied by a decrease in the chromosome number. The reduction in number has presumably taken place by unequal translocation in two chromosomes and the loss of the centromere in one of them by the method postulated by Darlington (1937) and later discovered in several organisms. This step would thus result in a karyotype like that found today in *Thereianthus* and *Micranthus* where there are a pair of long chromosomes. Further aneuploid reduction would result in the *Watsonia* karyotype with two pairs of long chromosomes.

The aneuploid reduction has been accompanied by a degree of morphological specialisation. The corm is short-lived in *Watsonia*, *Micranthus* and *Thereianthus* in contrast to the persistent type found in *Pillansia*. The evolution of the specialised genera from *Pillansia* is unlikely to have been direct, for the zygomorphic many-flowered *Micranthus* could not have given rise to the actinomorphic species of *Watsonia*. It is more likely that *Watsonia* represents one line and *Micranthus* another, both leading from *Pillansia* through *Thereianthus* where species with actinomorphic flowers predominate.

The bifid stigmas in this group were once regarded as an important taxonomic character and were the reason for *Lapeirousia* and *Freesia* being included in the tribe *Watsonieae* of Pax. The cytological data does not necessarily support this treatment, for although *Freesia* has 22 somatic chromosomes and several *Lapeirousia* species have a diploid number of 20, the karyotypes are unlike those found in *Watsonia* and its allies where the same numbers occur. Bifid stigmas also occur in species of *Crocus*; they are a characteristic feature of *Romulea* and are found in some species of *Crocosmia* such as *C. aurea* and in *Oenostachys dichroa* (Bullock 1930). *Romulea* and *Crocus* do not appear to be allied to the *Watsonia* group and neither does *Crocosmia*. These are more likely examples of parallel evolution, and it seems quite possible that bifid stigmas evolved independently in *Lapeirousia* and *Freesia* so that they should not be used alone as evidence of phylogenetic relationship.

In her classification, Lewis (1954) placed *Pillansia* in its own subtribe *Pillansiineae*, and *Watsonia*, *Thereianthus* and *Micranthus* with *Freesia* and *Lapeirousia* in the *Watsoniineae*. This treatment, in which Lewis recognises the relationship between *Watsonia* and *Pillansia*, is not followed for it is proposed that *Pillansia* be included in the *Watsoniineae*. *Freesia* and *Lapeirousia* are excluded from the group as it is believed that they are not very closely allied to *Watsonia*.

b. Subtribes ***Lapeirousiineae and Freesiineae***
Lapeirousia, Anomatheca & Freesia

This group comprises two discordant elements, *Lapeirousia* proper, i.e. the subgenera *Sophronia* and *Lapeirousia* (*Ovieda* of Baker) and *Freesia* and *Anomatheca*, previously the subgenus *Anomatheca* of *Lapeirousia*. Both groups are small herbaceous geophytes occurring throughout southern Africa. They differ consistently in several significant features which will be discussed in detail below. The three genera are dealt with together here, because they have, in the past, been regarded as closely allied, the main reason for this being the nature of the style branches which, in both genera, are deeply forked.

LAPEIROUSIA

(including only subgenera *Lapeirousia* (*Ovieda*) and *Sophronia*)

2n = 20, ?18.

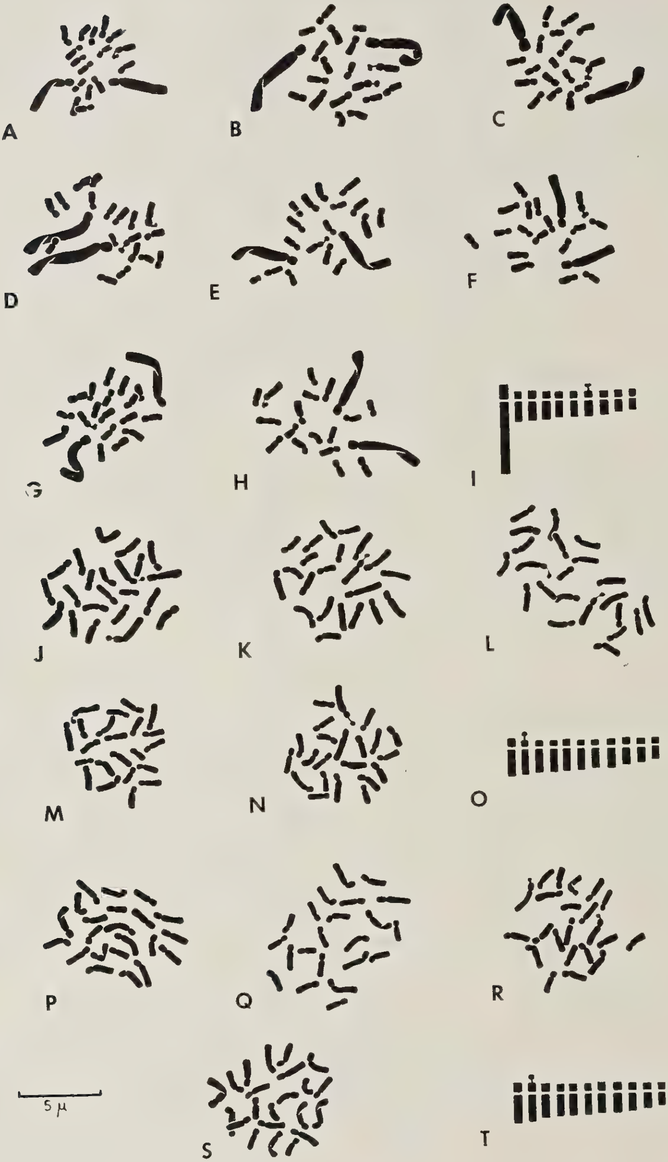
The genus, as circumscribed in this paper, i.e. excluding subgenus *Anomatheca*, comprises plants having a bell-shaped corm with a woody, entire tunic, a single basal leaf and large herbaceous floral bracts. The flowers, though very varied, are usually long tubed and have forked style branches.

There are about thirty species in the two subgenera. Eight of the approximately twenty species which occur in the winter rainfall area of the Cape Province were examined cytologically. The diploid number was clearly 20 in some species (Table 9), while in others it could not be established with certainty, 18, 19 or occasionally 20 somatic chromosomes being seen in different cells. It seems likely that these species also have 2n = 20 and that owing to the very small size of the chromosomes, one or two were sometimes overlooked, possibly being masked by others lying over them. The likelihood that the diploid number is 18 rather than 20 has been rejected, though this cannot be established for certain with present methods of examination and it remains possible that the last chromosome pair are simply large satellites.

TABLE 9
Chromosome numbers in *Lapeirousia, Anomatheca* and *Freesia.*

Species	Diploid No.	Collection Data or Reference
LAPEIROUSIA		
Subgenus 1. Sophronia		
L. oreogena Schlechter ex Goldblatt ined.	ca 18	Nieuwoudtville, C.P. *Goldblatt 245*
Subgenus Lapeirousia (=Ovieda Baker)		
L. corymbosa (L.) Ker	20	Tulbagh, C.P. *Goldblatt 203*
L. micrantha Meyer ex Klatt	20	Giftberg, C.P. *Goldblatt 374*
L. fastigiata (Lam.) Ker	20	Paarl flats, C.P. *Goldblatt 456*
L. fissifolia (Jacq.) Ker	ca 20	Montagu, C.P. *Goldblatt 428*
L. jacquinii N. E. Br.	ca 20	Piketberg, C.P. *Goldblatt 232*
L. anceps (L.f.) Ker	20	
L. divaricata Bak.	ca 20	
ANOMATHECA		
A. laxa (Thunb.) Goldblatt	22	Inhaca Island, Mozambique. *Goldblatt 1* (J)
(as Lapeirousia cruenta)	16	(Brittingham 1934)
(as L. cruenta)	22 (publ. in error as 20.)	(Dyer 1963)
A. grandiflora Bak.	22	Johannesburg, Tvl. *Goldblatt, 8, 9* (J)
A. verrucosa (Vog.) Goldblatt (=A. juncea)	22	near Avontuur, C.P. *Goldblatt 451.*
A. fistulosa (Spreng. ex. Klatt) Goldblatt	22	Camps Bay, C.P. *Goldblatt 517*
A. viridis (Lindl.) Goldblatt	22	Saldanha district, C.P. *Goldblatt 252*
FREESIA Klatt		
F. elimensis L. Bol.	22	Bredasdorp, C.P. *Goldblatt 379*
F. muirii N. E. Br.	22	Southern C.P. *Goldblatt 145* (J) (ex hort)
F. c.f speciosa L. Bol. (non flowering material)	22	Ladismith, C.P. *Goldblatt 491*
F. refracta (Jacq.) Klatt	22	Worcester, C.P. *Goldblatt 143* (J)
	22	(Taylor 1926)
F. cultivars	22, 33	(Brittingham 1934)

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Unless stated to the contrary, material is housed at the Bolus Herbarium, Cape Town.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
5 μ
S
T

In one species, *L. oreogena* (subgenus *Sophronia*) only 18 chromosomes could be detected, but whether this really represents a difference between it and the other species examined, all of which belong to subgenus *Lapeirousia*, is uncertain because of difficulties in counting the smallest chromosomes.

The karyotype of *Lapeirousia* is remarkable in that it consists of a single pair of very large chromosomes and the remainder (whether eight or nine pairs) are all very small. One or sometimes two satellites are found on short chromosomes and are assumed to be a constant feature of the karyotype. The idiogram shown here (fig. 18: I) consisting of 10 chromosomes, is based on the karyotype of *L. corymbosa* and is assumed to be representative of the genus.

The karyotype is peculiarly asymmetrical in having the single pair of very large chromosomes. This pair of chromosomes are amongst the largest in the tribe *Ixieae* and more like those found in the *Irideae*. There are approximately twenty species in these two subgenera in the winter rainfall region of southern Africa and about ten more in the summer rainfall region of south and tropical Africa. Perhaps when more species are examined cytologically, particularly those in the summer rainfall region, none of which were available, intermediate karyotypes may be found, leading to the very asymmetrical one occurring in those winter rainfall specimens studied.

ANOMATHECA

2n = 22.

There are perhaps six or seven species in the subgenus, occurring in both summer and winter rainfall areas of southern Africa. *Anomatheca* is distinguished by its conical corms with reticulate fibres, several basal leaves and short rather membranous floral bracts. Five species were examined by the present author (Table 9). One species, *A. fistulosa* was previously referred to *Lapeirousia* but due to its karyotype and morphology it is treated as an *Anomatheca* here. In all five species a diploid number of 22 was obtained. The chromosomes are mostly acrocentric but some of the smaller ones are sub-metacentric. The chromosomes range in length from approximately 1,5 to 3μ. As in *Freesia*, in which the karyotype is very similar, there are two or three pairs of longer chromosomes (fig. 18: J—O).

The only species of *Lapeirousia* which has previously been cytologically examined, *A. laxa* is a member of the subgenus *Anomatheca*. Brittingham (1934) reported a diploid number of 16 for this species, known to him as *L. cruenta*.

Fig. 18.

Karyotypes and idiograms of *Lapeirousia*, *Anomatheca* and *Freesia*. A. *Lapeirousia oreogena;* B. *L. corymbosa;* C. *L. micrantha;* D. *L. fastigiata;* E. *L. fissifolia;* F. *L. jacquinii;* G. *L. anceps (fabricii);* H. *L. divaricata;* I. Idiogram of *Lapeirousia;* J. *Anomatheca laxa;* K. *A. grandiflora;* L. *A. juncea;* M. *A. fistulosa;* N. *A. viridis;* O. Idiogram of *Anomatheca;* P. *Freesia refracta;* Q. *F. muirii;* R. *F. elimensis;* S. *F. cf. speciosa;* T. Idiogram of *Freesia.*

Dyer (1963) reported a diploid number of 20 for the same species (also as *L. cruenta*). This report of 2n = 20 is a typographical error for Dyer (private communication) has stated that the diploid number is 22. Dyer (private communication) also found that the karyotype consisted of small chromosomes with one pair of satellite chromosomes which thus appeared rather larger.

Brittingham's report of 2n = 16 for *A. laxa* seems in light of the present author's confirmation of Dyer's report, to be erroneous and it appears that Brittingham may have misinterpreted the karyotype of this plant.

FREESIA

2n = 22.

Freesia is a small genus comprising at present about twenty species. It is in need of revision for there are without doubt fewer species than are recognised today. It is similar in most respects to *Anomatheca*, differing mainly in having a horizontal, inflexed inflorescence, and scented flowers with a long bottle-shaped perianth tube. Four species were examined by the present author and in all a diploid number of 22 was obtained. The chromosomes are acrocentric and range in size from 1,5 to 3μ. Although the chromosome length forms a continuous series, two or three pairs of larger chromosomes can be distinguished and satellites appear to be located on one of these pairs (fig. 18: P—T).

The karyotype of *Freesia* was first described by Taylor (1926) who found a diploid number of 22 in a horticultural form of *F. refracta*. Brittingham (1934) also examined horticultural stock and found diploid numbers of 22 in several cultivars and 44 in another. The present study confirms that the basic number for the genus is 11 but the counts for the four species studied here are new records for wild species.

The status of *Anomatheca*.

Anomatheca was a genus established by Ker (1805) for *A. verrucosa* (as *A. juncea*) previously regarded as a *Gladiolus*. The main reasons for the creation of the genus were the bifid stigmas, reticulate corm tunics and the peculiar rough surfaced capsule, all features being quite unlike those found in *Gladiolus*. *Anomatheca* was recognised by Baker (1876) but later he reduced it to the rank of a subgenus in *Lapeirousia* (Baker 1892). This treatment was followed in *Flora Capensis* and has subsequently been maintained.

Lewis (1954) considered that *Lapeirousia* sensu Baker was an unnatural group and suggested that *Anomatheca* was in fact more closely related to *Freesia* than to the rest of *Lapeirousia*. This opinion is supported by the present author on cytological and morphological grounds and *Anomatheca* is reinstated here as a valid genus. It is very closely related to *Freesia* and if there is to be consistancy in the treatment of genera the two should perhaps be merged.

Excluding *Anomatheca*, *Lapeirousia* consists of plants which have the following characteristics: a distinctive flat based corm with hard entire tunics; one or two basal leaves; an inflorescence frequently much ramified; actinomorphic or zygomorphic flowers with bifid stigmas and a capsule with a smooth, membranous surface. *Anomatheca* has in contrast a round based corm with reticulate tunics, several basal leaves, only one or two branches on the inflorescence and zygomorphic flowers with a long perianth tube and a distinctive rough surface capsule. *Freesia* has all these features which are characteristic of *Anomatheca* and the only difference between the two is in the form of the perianth tube. In *Freesia* the tube is elongate-infundibuliform and in *Anomatheca* varies as it is either turbinate or curved with a wide throat. These differences are of a minor nature and do not seem to constitute a reason for separating the genera.

The cytological evidence supports the contention that *Freesia* and *Anomatheca* are closely related as they have a similar karyotype with a diploid number of 22. The remainder of the species of *Lapeirousia* has a quite different and distinctive karyotype and with the suggested diploid number of 20. The intergeneric crosses attempted by the author between *Freesia* and *Anomatheca* did not succeed. Further crosses should be attempted, especially between other species in the two genera. The failure of the crosses does, however, constitute a piece of evidence against the contention of a very close relationship between *Freesia* and *Anomatheca*, because most species in genera in the *Ixieae* are interfertile. If more crosses are tried and fail, then the two genera should perhaps be maintained as separate entities. If, however, these succeed the possibility of merging *Freesia* and *Anomatheca* should be seriously considered.

The position of *Lapeirousia fistulosa*

Lapeirousia fistulosa is a fairly well-known plant which has long been considered as belonging to the subgenus *Lapeirousia*. The discovery that its karyotype was like that of *Anomatheca* prompted a close examination of the plant. It is rather small and reduced and often bears a single flower. When it has more than one flower these appear pedicellate but the flowers should rather be considered as solitary branches. This accords with the occurrence of sessile flowers in the whole of the tribe *Ixieae*. The corm of this species is small and spherical but the tunics are clearly of reticulate fibres and not woody as in *Lapeirousia* proper.

This species has only two well-developed leaves and these are broad and soft in texture and quite unlike those found in most species of *Lapeirousia* where only one rigid and ribbed leaf occurs. The bracts are fairly small and rather dry like those found in *Anomatheca*. One feature which does not agree with this subgenus is the capsule. This in *Anomatheca* is typically broader than high, has a rather firm, rough papillate outer surface and contains large ovoid seeds. *Lapeirousia fistulosa* has a rather elongated smooth walled capsule containing small angled seeds. This latter type of fruit is found in *Lapeirousia* (sensu stricto) and also in many other genera such as *Hesperantha* and *Tritonia*. Both morphological and cytological evidence are strongly in favour of the transfer of this species to *Anomatheca*, which must itself be slightly expanded in concept to include this somewhat reduced plant.

The relationship between *Lapeirousia* and *Anomatheca* and *Freesia*

The relationship between *Anomatheca* and *Freesia* on the one hand and *Lapeirousia* (sensu stricto) on the other, is not, in the present author's opinion, a close one. The only feature in common is the bifid stigma which, as discussed under *Watsonia*, is believed to have evolved independently at least twice in the family, and is probably not as important a feature as was previously believed. The type of corm and the nature of the corm tunics are a far more reliable taxonomic character at generic level. In this feature, *Lapeirousia* is different from most of the other *Ixieae*, having a bell-shaped corm with entire and usually hard tunics. Other groups which have the most similar type of corm are *Hesperantha* and its allies, and *Romulea*. In these genera the corm has hard, entire tunics but with a smooth surface in contrast to *Lapeirousia* in which the surface is rather rough. In *Hesperantha*, its allies and *Romulea* the corm usually consists of one or only a few internodes and the roots emerge from only one side of the base of the corm which is extended to form a ridge so that these corms can be described as asymmetric, though some species of Romulea have a circular basal ridge. In *Lapeirousia* the corm also consists of very few internodes, but the roots emerge from all sides of the base of the corm.

Thus, a relationship between *Lapeirousia* and *Hesperantha* and its allies as suggested by the similarity of their corms is not as close as appears at first. *Lapeirousia* has frequently been grouped with *Watsonia* owing to the bifid nature of the stigmas in both of them. There are, however, no other indications of close relationship.

The type of corm with several internodes in *Freesia* and *Anomatheca* occurs in most genera of the *Ixieae* but the reticulate tunics are less common. *Sparaxis*, *Ixia* and *Tritonia* have a corm most like that of *Anomatheca* and this may indicate some relationship between them. Karyologically *Freesia* and *Anomatheca* appear to be allied to *Tritonia* ($2n = 22$) and less to *Ixia* and *Sparaxis* ($2n = 20$). There is, however, no strong evidence to indicate the affinity between *Freesia* and *Anomatheca* on the one hand and any particular group in the *Ixieae* on the other. Accordingly the new subtribe *Freesiineae* is proposed for these two closely allied genera.

TABLE 10

Chromosome numbers in *Schizostylis, Hesperantha, Geissorhiza, Engysiphon* and *Melasphaerula*

Species	Diploid No.	Collection Data or Reference
SCHIZOSTYLIS Backh. & Harv.		
S. coccinea Backh. & Harv.	26	Haenertsburg, Tvl. *Goldblatt 12* (J)
HESPERANTHA Ker		
H. baurii Bak.	26	Graskop, Tvl. *Goldblatt 72* (J)
H. longituba (Klatt) Bak.	26	Graskop, Tvl. *Goldblatt 73* (J)
H. radiata (Jacq.) Ker.	26	Touws River, C.P. *Goldblatt 146* (J)
H. angusta (Jacq.) Ker.	26	Nieuwoudtville, C.P. *Goldblatt 229*
H. buhrii L. Bol.	26	Nieuwoudtville, C.P. *Goldblatt 243*
H. falcata (L.f.) Ker.	26	Cape Point Reserve, C.P. *Goldblatt 149* (J)
H. pilosa (L.f.) Ker.	26	Grasberg, near Nieuwoudtville, C.P. *Goldblatt 272*
H. puberula Schltr.	26	Nieuwoudtville, C.P. *Goldblatt 284*
H. flexuosa Klatt	26	Springbok, C.P. *Goldblatt 191*
H. vaginata (Sweet) Goldblatt	26	Nieuwoudtville, C.P. *Goldblatt 259*
H. vaginata (Sweet) Goldblatt (=H. stanfordiae)	26	Nieuwoudtville, C.P. *Goldblatt 93* (J)
H. pauciflora (Bak.) Lewis	26	Nieuwoudtville, C.P. *Goldblatt 231*
H. spicata (Burm. f.) N. E. Br.	26	Darling, C.P. *Goldblatt 416*
GEISSORHIZA Ker.		
G. splendidissima Diels	26	Nieuwoudtville, C.P. *Goldblatt 347*
G. louisabolusii Foster	26	Citrusdal, C.P. *Goldblatt 247*
G. imbricata (de la Roche) Ker	26	(ex hort) *Goldblatt 165* (J)
G. aspera Goldblatt (=G. secunda)	52	Signal Hill, C.P. *Goldblatt 213*
	52	Simonstown, C.P. *Goldblatt 520*
(as G. secunda)	26	(Gwynn 1958)
G. heterostyla L. Bol.	26	Voëlvlei, Sutherland, C.P. *Hall* (NBG)
G. inaequalis L. Bol.	52	Van Rhyns Pass, C.P. Nieuwoudtville, C.P. *Goldblatt 129* (J), *275*
G. leipoldtii Foster	26	Calvinia, C.P. *Goldblatt 135* (J)
G. bolusii Bak.	39	Bains Kloof; Grootkop, C.P. *Goldblatt 458, 515*
G. pusilla (Andr.) Klatt	26	Signal Hill, C.P. *Goldblatt 196*
G. nana Klatt	26	Caledon, C.P. *Goldblatt 214*
G. ovata (Burm. f.) Asch. & Graeb.	26	Botrivier, C.P. *Goldblatt 217*
ENGYSIPHON Lewis		
E. exscapus (Thunb.) Lewis	26	Bains Kloof, C.P. *Goldblatt 483*
E. longifolius Lewis	26	Pakhuis Pass, Clanwilliam, C.P. *Goldblatt 122* (J)
E. brevitubus Lewis	26	Piketberg, C.P. *Goldblatt 204*
MELASPHAERULA Ker		
M. ramosa (L.) Ker N. E. Br.	22	Nieuwoudtville, C.P. *Goldblatt 110* (J)

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are housed at the Bolus Herbarium unless stated to the contrary.

Lapeirousia, excluding *Anomatheca*, is a natural group although it does include a wide range of species with different habit and flower type. The flower ranges from actinomorphic short-tubed as found in *L. corymbosa*, to zygomorphic and long-tubed, as occurring in *L. arenicola* and in *L. fabricii*, where the perianth tube is curved and broad at the apex. As *Lapeirousia* does not appear to be closely allied to any other genus in the *Ixieae*, and has such a distinct type of corm, it is proposed that it be placed in its own subtribe *Lapeirousiineae*.

c. Subtribe ***Hesperanthineae***

Hesperantha, Schizostylis, Geissorhiza, Engysiphon, Melasphaerula

The representatives of this group of genera are all small herbaceous plants, generally having hard, woody corm tunics and fairly unspecialised, usually actinomorphic flowers. *Schizostylis* is an exception, the rootstock being rhizome-like.

HESPERANTHA

$2n = 26$.

Hesperantha is a fairly large genus occurring from central to southern Africa. The species are mostly small plants with small, regular, often scented flowers which open in the afternoon and evening. The genus can be distinguished by its bell-shaped corms with hard, woody corm tunics, and characteristic laterally projecting ridge and the style which divides at the mouth of the perianth tube into three long branches.

In all twelve species of *Hesperantha* studied, of a total of about fifty species, a diploid number of 26 was obtained (Table 10). The chromosomes are acrocentric and relatively uniform in size, ranging from 1,3 to 2,5μ in length (fig. 19). Although it is often possible to distinguish a group of larger chromosomes, the number of these is not constant in all species and the size of individual chromosomes does not form any constant feature of the karyotype. Satellites are occasionally seen on one or two of the smaller chromosomes.

The only previous report on the cytology of the genus, that of Fernandes and Neves (1961) for *H. falcata*, is confirmed in the present study. It is clear that the basic number in the genus is 13.

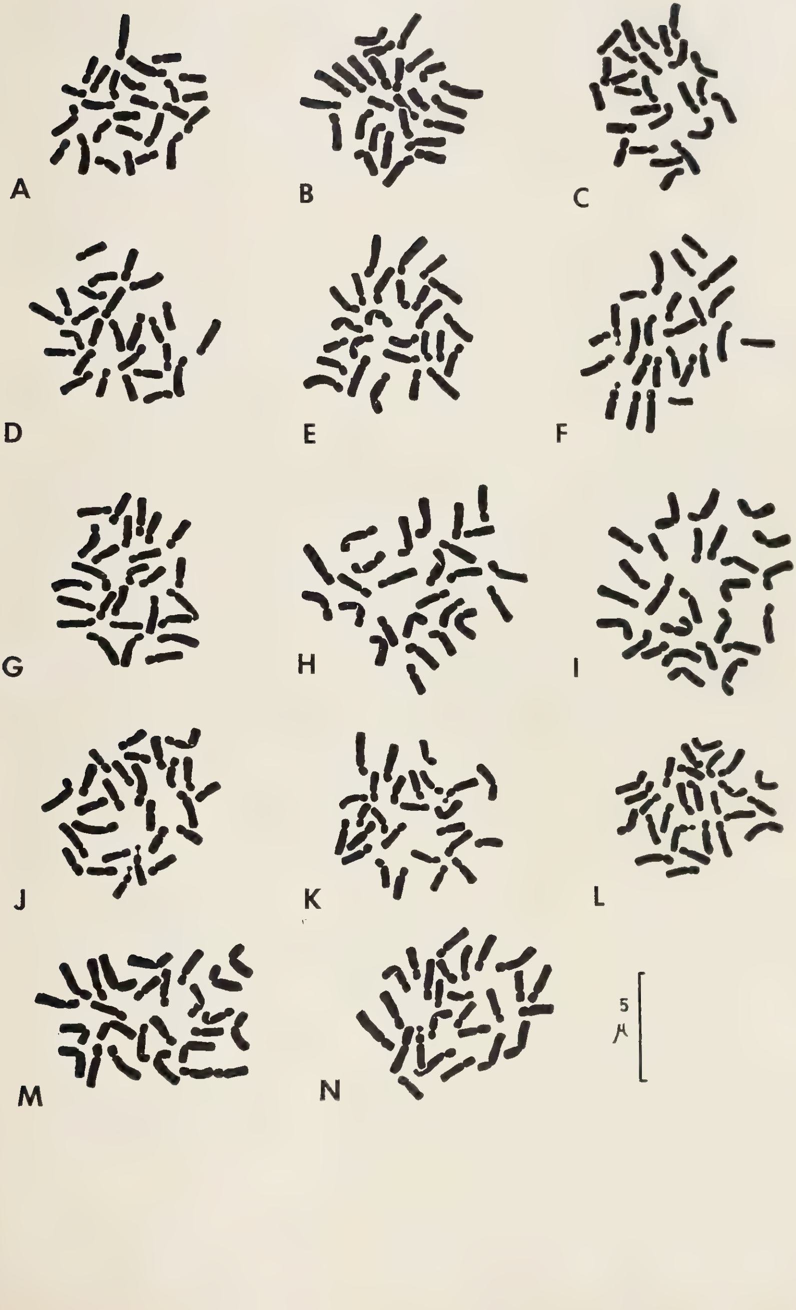
SCHIZOSTYLIS

$2n = 26$.

This is a small, possibly monotypic genus of streamside plants found in mountainous regions from central Africa to the eastern Cape Province. It is

Fig. 19.

Karyotypes of *Hesperantha* and *Schizostylis*. A. *Hesperantha baurii;* B. *H. longituba;* C. *H. radiata;* D. *H. angusta;* E. *H. buhrii;* F. *H. falcata;* G. *H. pilosa;* H. *H. puberula;* I. *H. flexuosa;* J. *H. vaginata;* K. *H. vaginata* (=*stanfordiae*); L. *H. pauciflora;* M. *H. spicata;* N. *Schizostylis coccinea.*


A
B
C
D
E
F
G
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I
J
K
L
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5 μ

very similar to *Hesperantha*, having the same characteristic flowers and style branches. The only difference is the rootstock which in *Schizostylis* is a short thick rhizome-like structure.

One of the two doubtfully distinct species, *Schizostylis coccinea*, was examined cytologically for the first time. The diploid number was found to be 26 and the karyotype, which resembles that of species of *Hesperantha*, consists of acrocentric chromosomes which range from 1,2 to 2,5μ in length (fig. 19: N).

GEISSORHIZA

2n = 26.

Geissorhiza is a genus of about fifty species, occurring in the winter rainfall area of southern Africa. It is allied to *Hesperantha* which it closely resembles. The differences are that the style forks well beyond the mouth of the perianth tube and the style branches are shorter. The hard, overlapping corm tunics have a tendency to split vertically giving the corm a tiled appearance, a feature often useful in identification of non-flowering material.

Eleven of the approximately forty-five species in the genus were examined (Table 10). A diploid number of 26 was obtained in eight species. Of the remainder, *G. bolusii* was found to have 39 somatic chromosomes and both *G. aspera* and *G. inaequalis* have 52 somatic chromosomes. In all the species examined, the chromosomes were acrocentric, sometimes tending to be submetacentric, and relatively uniform in size, ranging in length from 1,2 to about 2,5μ (fig. 20: A—K). The size was found too uniform to allow recognition of groups of small or large chromosomes. Satellites were sometimes observed on one or two chromosomes of intermediate size. The chromosome numbers found in the genus indicate that the basic number is 13. The karyotype is very similar to that of *Hesperantha* and confirms the view that these two genera are closely related.

There has been only one previous report on the cytology of *Geissorhiza*, when Gwynn (1958) found a diploid number of 26 for *G. aspera* (as *G. secunda*). The present author's findings confirm this number for the genus but not for that particular species. Because polypoloidy was found to be rare in the tribe *Ixieae*, particularly in the species of the winter rainfall region, the occurrence of three polyploid species in *Geissorhiza* caused some surprise. Separate populations from distant localities were therefore examined. The additional populations of *G. aspera*, *G. inaequalis* and *G. bolusii* were found to have the same level of polyploidy as those previously studied. Although meiotic studies were not made, it appears that *G. aspera* and *G. inaequalis* are tetraploid species. They are known to be fully fertile. It is possible that the plant studied by Gwynn was a diploid individual of *G. aspera* or it may have been confused with another species.

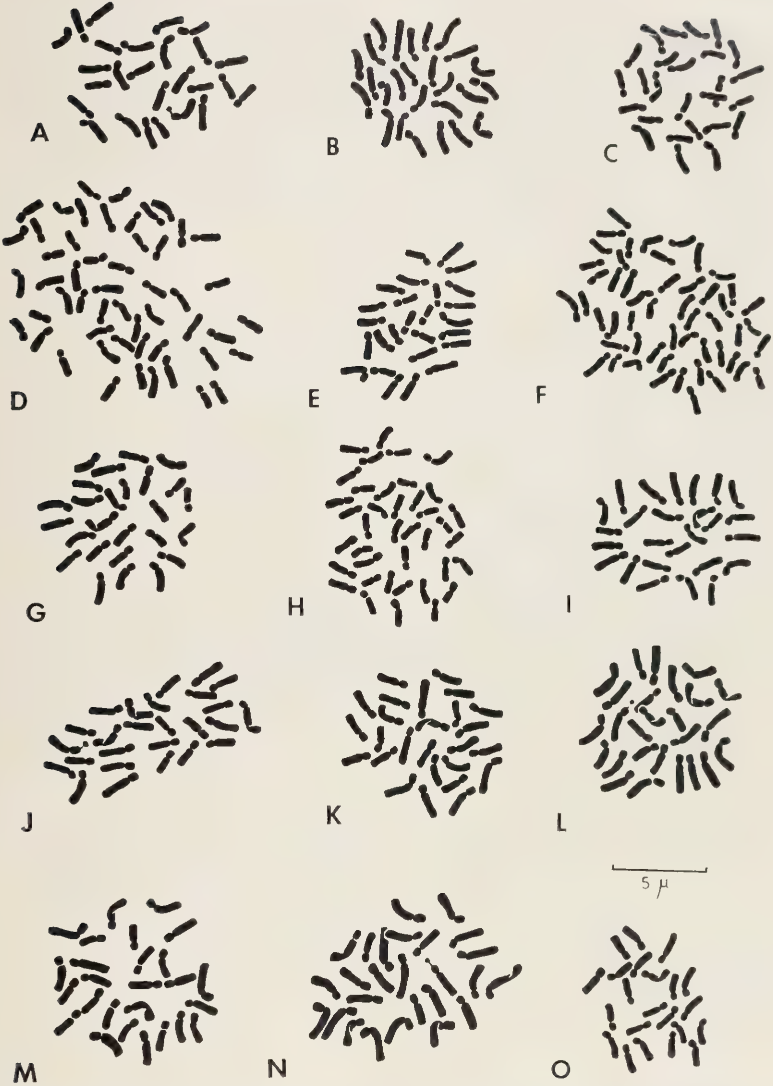

Fig. 20.

Karyotypes of *Geissorhiza*, *Engysiphon* and *Melasphaerula*. A. *Geissorhiza splendidissima;* B. *G. louisabolusii;* C. *G. imbricata;* D. *G. aspera;* E. *G. heterostyla;* F. *G. inaequalis;* G. *G. aff. leipoldii;* H. *G. bolusii;* I. *G. pusilla;* J. *G. nana;* K. *G. ovata;* L. *Engysiphon brevitubus;* M. *E. exscapus;* N. *E. longifolius;* O. *Melasphaerula graminea.*

Geissorhiza bolusii is a sexually sterile species which is similar, and probably identical to *G. rupestris*, another species which does not produce seed. Flowers are sometimes produced but seed is never set. Instead small cormlets are produced in the axils of the bracts on the inflorescence, sometimes after flowering has occurred or in place of the flower. In view of the vegetative apomixis found in this plant, it came as no surprise that it was found to be triploid. Populations from both Bains Kloof and the Cape Peninsula had 39 chromosomes and with the sexual sterility in this plant it is likely to be a naturally occurring triploid species. The cormlets appear to have assumed the function of seeds and are presumably dispersed in a similar way.

ENGYSIPHON

2n = 26.

Three species of the small genus *Engysiphon*, a segregate of *Geissorhiza*, were examined (Table 10). The genus, which is found only in the south western Cape, is distinguished from *Geissorhiza* by its larger, usually long tubed flower and its larger asymmetrical corm. All three have a diploid number of 26 and a similar karyotype consisting of rather uniform acrocentric chromosomes which range in size from 1,0 to 2,5μ in length (fig. 20: L—N). The karyotype is indistinguishable from that of *Hesperantha* and *Geissorhiza*, and indicates a close relationship between these genera.

MELASPHAERULA

2n = 22.

Melasphaerula is a monotypic genus, widespread in the south western Cape. The plant has a symmetrical corm with hard entire tunics. The scape is highly ramified, and bears large numbers of small, dull coloured zygomorphic flowers. *M. graminea* was found to have a diploid number of 22, with predominantly acrocentric chromosomes more or less uniform in size (fig. 20: O) from 1,3 to 2,0μ in length.

Intergeneric hybridisation

Attempts to obtain intergeneric hybrids in this group of genera were rather unsuccessful (Table 1). A cross between *Geissorhiza leipoldtii* aff. and *Hesperantha falcata* failed, and although *Schizostylis coccinea* hybridised with *Hesperantha falcata*, the number of seeds in the fruit was reduced, and the seed failed to germinate. This is perhaps an indication of a small degree of compatibility between these two genera, and can be regarded as evidence of their suggested close relationship.

Discussion

It is clear that the basic number of *Schizostylis*, *Hesperantha*, *Geissorhiza* and *Engysiphon* is 13 and that they have very similar karyotypes which should be regarded as evidence of their close relationship to one another.

The basic number in *Melasphaerula* is 11 and it is probably not very closely related to the other genera. It has been placed in this section mainly on morphological grounds. *Melasphaerula* is a rather unusual member of the tribe *Ixieae* and does not fit conveniently in any classification of the group. The plant is very branched and has zygomorphic flowers and a peculiar three winged capsule. One feature which indicates its relationship is its corm which has hard entire tunics which in old plants are split and lie on top of the newer tunics. Although the corm tunics resemble those of *Geissorhiza*, the corm is not asymmetric as it is in *Geissorhiza* and its immediate allies.

Taxonomic position of *Schizostylis*

Schizostylis has long been regarded as the probable ancestor of the above group of genera. It has all the floral characteristics of *Hesperantha* but lacks a true corm. Instead, the rootstock is a somewhat short, thick rhizome which has an entire but papery covering. This structure has been regarded as the forerunner of the asymmetrical corm of *Hesperantha* with its entire but woody tunic (Lewis 1954).

Schizostylis produces small propagules which are remarkably like tunicate corms in the axils of the scape. This fact suggests a possible alternative interpretation of the rootstock which may be an expanded corm and rhizome-like as a secondary development. As corms are essentially modified to survive dry conditions it seems a plausible argument that *Schizostylis*, a streamside plant, may have lost its corm due to the semi-aquatic conditions under which it grows. Some species of *Hesperantha* and *Geissorhiza* also grow in marshy places and have retained their corm but in this case the wet area dries out completely during the dry season.

Since the first classification of the Iridaceae by Bentham & Hooker (1883) *Schizostylis*, *Hesperantha*, and *Geissorhiza* have been placed together in the same tribe or subtribe. The only exception to this was made by Hutchinson (1934) who placed *Schizostylis* together with *Aristea* in a tribe quite separate from *Hesperantha* and *Geissorhiza*. The basis for this treatment was the absence of the corm in *Schizostylis*. This has since been refuted by Lewis (1954) on purely morphological grounds because *Hesperantha* and *Schizostylis* are identical except in their rootstock, and as explained above, even this difference is not necessarily fundamental. Indeed, whatever the nature of the rootstock it is quite clear from both morphological and cytological evidence that these two genera are very closely allied, and except for this vegetative difference, would surely be placed in a single genus.

The validity of *Engysiphon*

Engysiphon is a relatively new genus which was described by Lewis (1941) as a segregate of *Acidanthera*, an artificial collection of species grouped together by Baker (1896). Lewis showed that the South African species placed in *Acidanthera* belonged either to *Gladiolus*, *Hesperantha*, *Tritonia* or were allied to *Geissorhiza*. These latter species she placed in the new genus *Engysiphon*. The genus differs from *Geissorhiza* in having large slightly zygomorphic flowers with long narrow perianth segments. *Geissorhiza* typically has smaller flowers which are actinomorphic. The perianth tube is also far longer in most species of *Engysiphon* than in *Geissorhiza*.

Cytological investigation has shown that Lewis was correct in her treatment of *Acidanthera* for species placed in *Gladiolus* and *Tritonia*, namely *G. praelongitubus* and *T. flabellifolia* were found to have a karyotype resembling those of the rest of the species of the genera to which they were referred. *Engysiphon* has proved to have a basic number of 13 and a karyotype like *Geissorhiza*. In reviewing the validity of many genera in the Iridaceae it seems that *Engysiphon* is hardly sufficiently distinct from *Geissorhiza* to merit recognition, as far greater variation in flower structure occurs in most other genera than exists between *Geissorhiza* and *Engysiphon*. There is little doubt, however, that the distinction is very convenient because *Geissorhiza* is a large genus and the identification of species in this group is already very difficult.

Conclusion

The present study confirms Lewis' classification of the five genera in this section. She placed the four genera which have a basic number of 13 in a single phylogenetic line beginning with *Schizostylis* and leading to *Hesperantha* and then independently to *Geissorhiza* and *Engysiphon*, where a small degree of zygomorphy is achieved in the flower. She placed *Melasphaerula* at the end of a separate line separating quite early from the main sequence leading to *Geissorhiza*. Lewis continued her line from *Geissorhiza* to *Gladiolus* and its allies for she believed that *Gladiolus* was derived from *Geissorhiza* and that the two genera actually merged together. This will be discussed later under *Gladiolus*.

Melasphaerula does not fit in the same phylogenetic line but the nearest related genus appears to be *Geissorhiza*. It is more specialised than *Geissorhiza* in that the flowers are zygomorphic. Also the capsule is rather different from the fruits in the remainder of the tribe.

Lewis placed all these genera together with *Dierama*, *Ixia*, *Tritonia* and their allies in her subtribe *Ixiinieae*. She did not divide up this large subtribe further for she remarks that further subdivision would result in artificial grouping of genera. The karyological results do, however, refute this statement and have shown that within Lewis' *Ixiinieae* there are several distinct karyotypes each one usually shared by a group of genera which are morphologically similar. *Schizostylis*, *Hesperantha*, *Geissorhiza* and *Engysiphon* form a natural unit, all having a karyotype with 26 chromosomes and can conveniently be grouped in a separate subtribe which the present author proposes to name *Hesperanthineae*. *Melasphaerula* does not fit perfectly into this subtribe but rather than create a separate subtribe for a single species it has been placed here in the group to which it seems most closely related.

TABLE 11

Chromosome numbers in *Romulea* and *Syringodea*.

Species	Diploid No.	Collection Data or Reference
ROMULEA Maratti		
R. hantamensis (Diels) Goldblatt	30	Calvinia, C.P. *Goldblatt 276*
R. sabulosa Beg.	26	Nieuwoudtville, C.P. *Goldblatt 96* (J)
R. minutiflora Klatt	26	Krom River, Cedarberg, C.P. *Goldblatt 230*
R. flava (Lam) de Vos	24	Simonsberg, C.P. *Goldblatt 41* (J)
(as R. bulbocodioides)	18	(Gwynn 1958)
R. ochroleuca unpublished name	18	(Gwynn 1958)
R. rosea Eckle	18	(Gwynn 1958)
R. rosea var. parviflora Bak.	18	Stellenbosch, C.P. *Goldblatt 138* (J)
R. atrandra var. luteoflora de Vos	22	Calvinia, C.P. *Goldblatt 277*
R. triflora (Burm, f.) N.E. Br.	20	Ceres district, C.P. *Goldblatt 317*
R. columnae (as R. parviflora)	60	Matsuura and Suto (fide Darlington and Wylie 1955)
R. bulbocodium	34	Fernandes et al. (fide Darlington and Wylie 1955)
(The large number of species examined by de Vos 1965 is not included here)		
SYRINGODEA Hook. f.		
S. longituba (Klatt) O. Kuntze	12	Albany district, C.P. *Bayliss 2182* (NBG)
S. montana Klatt	12	Giftberg, C.P. *Barker 10210* (NBG)
S. unifolia Goldblatt (ined.)	22	Matroosberg, C.P. *Stayner s.n.* (NBG 87602)

All localities are in the Cape Province (C.P.), South Africa. Unless otherwise stated, specimens are located at the Bolus Herbarium, Cape Town.

d. Subtribe *Crocineae*

Romulea, Syringodea, Crocus

This group comprises small plants which have reduced inflorescences. The flowers are reduced to one per branch of the inflorescence, and often the aerial part of the scape is so reduced that the ovary is subterranean. The corms are either hard and woody, or somewhat papery, but entire, the leaves terete to bifacial and the flowers actinomorphic, usually with modified style branches.

ROMULEA

2n = 30—18.

Romulea is a large genus of approximately ninety species occurring from the Mediterranean, along the mountains of Africa to the Cape where most species are found. The genus consists of small reduced plants, the inflorescence of which can be regarded as solitary flowered, although the scape is often branched. The corms are small, with hard woody tunics and are often very characteristically shaped. The leaves are very distinctive in this genus, being slender, terete or sub-terete and having four channels running the length of the leaf. The flowers are actinomorphic often brightly coloured and usually short-tubed though some species have a perianth tube as long as five centimetres. The three style branches are usually deeply forked.

Romulea is one of the few genera in the *Iridaceae* in which the chromosome cytology has been extensively studied (de Vos 1965). Accordingly, only a few species were studied (Table 11) by the present author and a range of somatic chromosome numbers from 18 to 30 was found in these few species. The chromosomes are acrocentric and of comparable size in all the species examined, although somewhat smaller in species with a high chromosome number. There is little marked difference in size between the chromosomes of any species so that no distinctive karyotypes could be recognised (fig. 21: A—G).

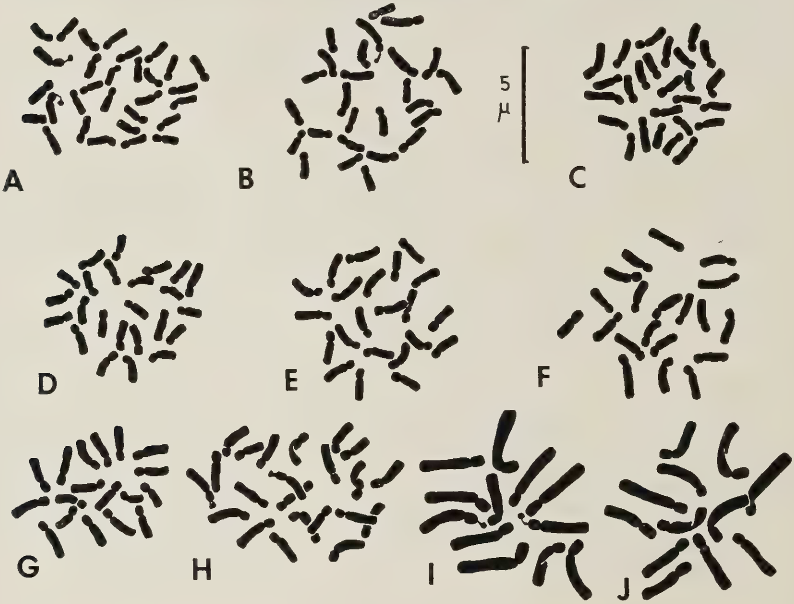

FIG. 21.

Karyotypes of *Romulea* and *Syringodea*. A. *Romulea hantamensis;* B. *R. sabulosa;* C. *R. minutiflora;* D. *R. flava;* E. *R. atrandra var. luteoflora;* F. *R. triflora;* G. *R. rosea var. parviflora;* H. *Syringodea rosea;* I. *S. longituba;* J. *S. montana.*

De Vos (1965) examined more than forty species and varieties including all but two of the species studied by the present author. Only the counts of 30 in *R. hantamensis* and 20 in a plant referred to *R. triflora* are new records for the genus. The counts for four of the other species confirm the results of de Vos but the present author obtained a diploid number of 22 in *R. atrandra* var. *luteoflora* while de Vos reported 2n = 20 for this variety although she found 2n = 22 in *R. atrandra* var. *atrandra*. An earlier cytological report for *Romulea* is that of Gwynn (1958) who found 2n = 18 in *R. rosea*, *R. ochroleuca* and *R. flava* (as *R. bulbocodioides*). This latter record is the only one not confirmed by de Vos. She found 2n = 24 in several varieties of *R. flava* (as *R. bulbocodioides*). It seems likely, with the difficulties of identification in *Romulea* that Gwynn was dealing with another species. Other records in *Romulea* are 2n = 60 for *R. parviflora* (apparently a synonym of *R. columnae*, a Mediterranean species), by Matsuura and Suto (fide Darlington & Wylie 1955), and 2n = 34 for *R. bulbocodium* (also a Mediterranean species) by Fernandes *et al.* (fide Darlington & Wylie 1955).

It is clear from these cytological studies that *Romulea* is a heteroploid genus. Apart from a few polyploid species which have chromosome numbers of 44 and 54 there is an aneuploid series ranging from 2n = 18 to 34. The majority of species in this series have a diploid number of 24 but several species have numbers of 26, 22 and 18.

The genus is still being studied by de Vos and was thus not investigated in any detail by the present author. It is, however, clear from the work of de Vos that cytology is proving an extremely valuable tool in resolving the many problems in this genus in which the taxonomy is notoriously difficult.

SYRINGODEA

2n = 22, 12.

Syringodea is a small genus known only from southern Africa. It appears to be related to *Romulea*, but the plants are more reduced, the flowers are fugaceous, usually solitary and an aerial stem is lacking. Unlike *Romulea* the terete leaves lack the grooves typical of that genus.

Three of the approximately ten species in the genus were studied (Table 11). The chromosomes are amongst the largest in the tribe *Ixieae*. One species, *Syringodea unifolia* has a diploid number of 22 and here the chromosomes are typical of the *Ixieae* in size and shape. In the two species with a diploid number of 12, the chromosomes are larger and almost of a size found in the *Irideae*, which are characterised by large chromosomes (fig. 21: H—J).

The genus *Syringodea* has not previously been examined cytologically. Like *Romulea* it appears to be heteroploid and until more species can be studied nothing can be said of the chromosome evolution in the genus. The comparatively large size of the chromosomes in *S. longituba* and *S. montana* are unusual and are largest in the tribe *Ixieae*. It is likely that they are the end result of decreasing aneuploidy. If so it would be expected that individual chromosomes would increase in size to prevent the loss of genetic material.

The taxonomic position of *Syringodea unifolia.*

Syringodea unifolia is an extremely unusual species. It has several characteristics which make it appear misplaced in its present genus. *Syringodea*, as generally accepted, comprises several small reduced plants with an almost symmetrical corm with woody tunics and a rosette of several slender, terete or sub-terete leaves. The flowers lack an aerial stem or peduncle and are raised above the ground by a long slender perianth tube. The flowers are usually small and soft textured and the style is divided into three short branches. The above species differs in most of these features. The corm is flattened in a vertical plane, being lens shaped with a crescent shaped ridge forming the periphery of the lower part of the lens. The plant bears a single, rather succulent terete leaf and the flower, though long tubed, is very large for the genus. Most unusual of all, the three style branches are themselves irregularly branched and divided.

This type of style is found in the genus *Crocus* (Maw 1882) and in one species of *Romulea* where bifid stigmas are the rule. The rather distinctive corm is characteristic of *R. tortuosa* and is not known in either *Crocus* or *Syringodea.* Argument can thus be led for transferring *Syringodea uniflora* to *Romulea*, for although a short perianth tube is the more usual of this genus, several species have a long tube and lack an aerial peduncle. An equally strong case can be made for the inclusion of this species in *Crocus*, where the peculiar shaped corm is the only difficulty. The leaf and flower are very characteristic of *Crocus* as is the stigma.

Cytological study does not appear to help in establishing the correct position or the plant. The small chromosomes are like those found in *Romulea* but the diploid number is quite different from *R. tortuosa* ($2n = 30$), the only plant that seems to have a similar corm. Too little is as yet known about the cytology of *Syringodea* but again the karyotype differs greatly between the two species studied here and *S. unifolia.* If *S. unifolia* is to remain in its present genus then both *Romulea* and *Syringodea* must be viewed in rather different terms. At present the main and diagnostic difference between these two genera is said to be the nature of the style branches; either entire in *Syringodea* or bifid in *Romulea* (Lewis 1954; Burtt 1967). The diagnostic character which now seems more significant is the leaf, being sub-terete in *Syringodea* and four-channelled in *Romulea.*

It is quite clear that all the other characters overlap, and it seems to indicate that *Syringodea* is probably a very specialised and reduced genus derived from *Romulea.* In an expanded definition of the genus, *S. unifolia* can then remain in its present position.

The subtribe *Croceae* sensu Bentham & Hooker.

Romulea and *Syringodea* are a pair of related genera which are both very reduced in size. In most species of *Romulea* only the pedicel extends above ground. In *Syringodea* this reduction has proceeded a step further for here the perianth tube serves to raise the flower above ground level. This reduction of the inflorescence and general size of the plant occurs in two other genera of the Iridaceae, namely *Galaxia* and *Crocus*, and this feature prompted Bentham & Hooker to group them together in a single subtribe which they placed in their tribe *Sisyrinchieae* together with *Aristea* and *Bobartia.* Pax (1888) raised this subtribe to the rank of subfamily but other workers followed Bentham & Hooker's concept. Hutchinson also recognised this grouping and made it one of his eleven tribes.

It remained to Lewis (1954) to point out the true affinities of these four genera. She shows clearly that *Galaxia* is actually allied to *Homeria* for it has a corm and leaves like *Moraea* and *Homeria.* The reduced size and inflorescence can thus be regarded as a case of parallel evolution. Lewis believed that *Romulea* and *Syringodea* were related and that they belonged in the tribe *Ixieae*, for though rather modified in many features, they have a corm very like that in *Hesperantha* and *Geissorhiza.* Both these suggestions made by Lewis are confirmed by cytological observations, for as explained earlier, *Galaxia* has the large chromosomes typical of the tribe to which *Moraea* and *Homeria* belong, while *Romulea* has small chromosomes which are typical of the *Ixieae. Syringodea* has chromosomes which are comparatively large but still appear to belong to the group with small chromosomes.

The taxonomic affinities of *Crocus*

The taxonomic position of *Crocus* is somewhat doubtful. Plants in this genus, like *Romulea* and *Syringodea*, are very reduced and they have no aerial stem or peduncle. The genus which is Mediterranean and Middle Eastern in distribution, is believed to be derived from *Romulea* which is both African and Mediterranean in distribution (Burtt 1967). *Crocus* appears better referred to the *Ixieae* as it has the type of corm found in this tribe. However, few species of *Crocus* have the peculiar hard, woody asymmetric corm tunic found in *Romulea* and *Syringodea.* Also *Crocus* has a leaf which is bifacial whereas the leaf is sub-terete in *Syringodea* and in *Romulea* is monofacial and peculiar in being four-grooved. These and other morphological features indicate that if

Crocus is derived from *Romulea* or *Syringodea* it has since become very modified and that the relationship between them is not as clear as suggested by Lewis and by Burtt.

Crocus is another genus where the cytology has been quite well investigated. The studies of Mather (1932), Karasawa (1956), Feinbrun (1958) and others have revealed that it is karyologically very complex. There is a series of somatic numbers ranging from 6 to 30, but it is probable that both aneuploidy and polyploidy have occurred in the evolution of the genus. Species with the higher somatic numbers have smaller chromosomes which resemble somewhat those of most Ixioid genera in general appearance and size but those with low somatic numbers have very large chromosomes resembling the *Irideae*.

A diploid number of 8 has been suggested by Feinbrun as the ancestral number in *Crocus* on the grounds that 8 and multiples of 8 are the most common diploid numbers in the genus. Apart from the fact that it is perhaps easiest to derive all the reported somatic numbers from 8 there is no support for this hypothesis. Unfortunately, it is not possible as yet to assign a primitive position in the genus to any particular species or group of species.

All that can be said in our present state of knowledge is that if *Crocus* belongs to the *Ixieae* and was evolved from a *Romulea*-like plant, then species with the higher somatic numbers and smaller chromosomes probably represent the ancestral condition. Consequently species with lower somatic numbers and large chromosomes are derived from them and are advanced at least in their karyotype. This is merely hypothetical and the condition in *Crocus* is open to many other interpretations. If Feinbrun's suggestion is correct, however, then on cytological grounds the position of *Crocus* in the tribe of *Ixieae* is seriously challenged.

Further morphological and cytological study of *Crocus* is indicated, perhaps by European workers who can more easily obtain species in their natural state. Tentatively, it is suggested that the subtribe *Crocineae* (as *Croceae*) of Bentham & Hooker (*Romulineae* as proposed by Lewis), containing *Romulea*, *Syringodea* and *Crocus* be maintained until more information is discovered.

The origin of the *Crocineae*

Romulea and its reduced allies are presumably derived from a less specialised group with similar but less reduced characteristics. *Hesperantha*, *Geissorhiza* and *Engysiphon* are the only genera with an asymmetric corm like that found in *Romulea*, which is clearly the least modified genus in the *Crocineae*. In addition, the peculiar four-grooved leaf of *Romulea* occurs in species of *Geissorhiza* and *Engysiphon* where it becomes clear that this type of leaf is derived from the ordinary equitant type by a thickening of the margins and the region round the mid-vein. The unthickened portions thus form the grooves. Species of *Geissorhiza* also have relatively unspecialised flowers with a short perianth tube like those occurring in most species of *Romulea*.

Thus *Geissorhiza* has a strong claim to be very like the ancestor of *Romulea*. It is interesting to note that in both *Geissorhiza* and *Hesperantha* there are species in which the inflorescence is reduced to a solitary flower. In *Geissorhiza*, these species differ from *Romulea* in the possession of a simple stigma in contrast to the bifid stigmas in *Romulea*.

If a plant resembling a *Geissorhiza* is accepted as the ancestor of *Romulea* and thus of the *Crocineae*, several comments can be offered on the evolution of the karyotypes in *Romulea*. The somatic number in *Geissorhiza* and all its close relatives is 26 and a similar number can then be expected in the ancestral or least specialised species of *Romulea*.

The work of de Vos has shown that the chromosome number in *Romulea* is closely correlated with the appearance of the corm which varies considerably thoughout the genus. The simplest corm and the one from which all others are most easily derived is, according to de Vos, the kind found in *R. flava* and she suggests that this is the most primitive type. This contention is supported by the morphology of the plant for *R. flava* is a species in which the scape is often borne above ground though the flowers are still solitary on the branches. The somatic number in *R. flava* and others with this kind of corm is 24, a number close to that of *Geissorhiza*. Although a diploid number of 26 occurs in a few species of *Romulea*, 24 is far more common and as this number is correlated with putatively primitive characters it appears that this is the ancestral condition in the genus. Consequently a basic number of 12 is suggested for *Romulea*. Accepting this, it is clear that both ascending and descending aneuploidy have occurred though the latter has predominated, which is in accordance with the view of Stebbins (1950) that this is more common than increasing aneuploidy.

e. Subtribe *Gladiolineae*

Gladiolus, *Acidanthera*, *Radinosiphon*, *Homoglossum* (including *Petamenes*), *Oenostachys* and *Anomalesia* (including *Kentrosiphon*).

This complex consists of small to medium sized, herbaceous deciduous plants. The plants have a spherical to flattened, symmetrical corm with entire, but fairly soft papery tunics, although the old, outermost tunics often split and appear fibrous. The inflorescences are, with few exceptions secund and the seed is winged except in a few isolated species and in *Radinosiphon*. The flowers are large and colourful, usually zygomorphic and the three style branches are typically expanded and bilobed at the apex. Two genera, *Petamenes* and *Kentrosiphon*, are reduced to synonymy, being included in *Homoglossum* and *Anomalesia* respectively.

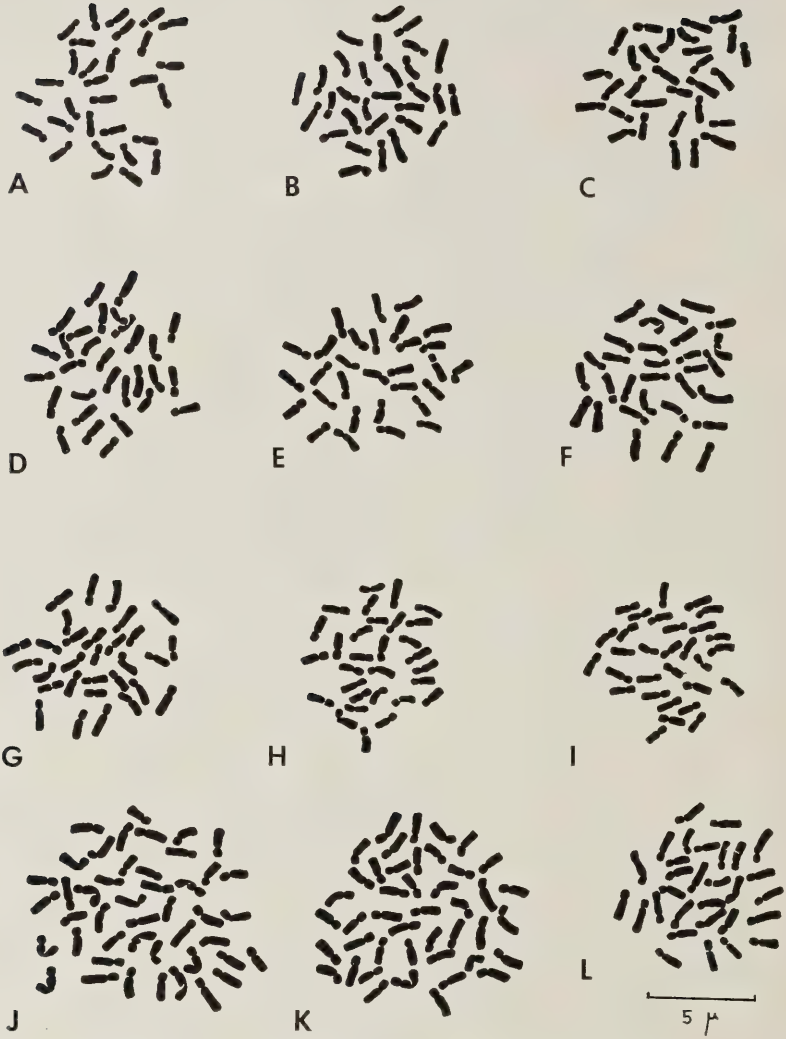

FIG. 22.

Karyotypes of *Gladiolus* and *Radinosiphon*. A. *Gladiolus pritzellii;* B. *G. undulatus;* C. *G. ceresianus;* D. *G. guinzii;* E. *G. brevifolius;* F. *G. edulis;* G. *G. crassifolius aff.;* H. *G. varius;* I. *G. praelongitubus*, J. *G. natalensis* (*psittacinus*), K. *G. natalensis var. cooperi;* L. *G. buckerveldii* (previously *Petamenes buckerveldii*).

TABLE 12
Chromosome Numbers in *Gladiolus.*

Species	Diploid No.	Collection Data or Reference
GLADIOLUS L.		
G. tristis L.	30	(Bamford 1935)
	30	(Mensinkai 1939)
G. pritzellii Diels	30	Nieuwoudtville, C.P. *Goldblatt 257*
G. undulatus Jacq.	30	Cedarberg, C.P. *Goldblatt 309*
	30	(Bamford 1935)
G. buckerveldii (L. Bol.) Goldblatt	30	Algeria, Cedarberg, C.P. *Jackson sn.* (NBG 85913)
G. ceresianus L. Bol.	30	Cold Bokkeveld, C.P. *Goldblatt 267*
G. gueizii (Kunze) Lewis	30	Cape St. Francis, C.P. *Basson s.n.* (NBG 88091)
G. brevifolius Jacq.	30	Kirstenbosch, C.P. *Goldblatt 523*
	30	(Bamford 1935)
G. edulis Burch ex Ker	30	Alice, Eastern C.P. *Goldblatt 369*
G. crassifolius Bak.	30	Mt. Anderson, Tvl. *Goldblatt 63* (J)
	30	(Bamford 1935)
G. varius Bol. f.	30	Graskop, Tvl. *Goldblatt 80* (J)
G. praelongitubus Lewis	30	Mt. Anderson, Tvl. *Goldblatt 64* (J)
G. natalensis (Eckl.) Reinw. ex Hook (=G. psittacinus)	45, 60, 75.	Inhaca Island, Mozambique. *Goldblatt 524* (J)
(as G. psittacinus)	90	(Bamford 1935)
G. natalensis var. cooperi Bak.	45, 60, 75.	Haenertsburg, Tvl. Raised from seed.
G. primulinus Bak.	60	(Bamford 1935)
	60	(Mensinkai 1939)
(n=30)		(Vilmorin and Simonet 1927)
G. dracocephalus Hook	90	(Bamford 1935)
	80	(Mensinkai 1939)
G. byzantinus Mill (n=30)		(Vilmorin and Simonet 1927)
	90	(Bamford 1935)
	60	(Mensinkai 1939)
G. illyricus Koch	90	(Bamford 1941)
	60	Portinho, Portugal (Hamilton 1968)
G. segetum Ker	120	(Bamford 1935)
	171±2	El Ronquillo, Spain (Hamilton 1968)
G. communis L.	±138	(Bamford 1935)
	180	(Bamford 1941)

(The large number of species studied by Bamford (1935; 1941) are not listed here.)

All localities are in South Africa unless otherwise stated. The provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are housed in the Bolus Herbarium, Cape Town, unless stated to the contrary.

GLADIOLUS

2n = 30, 45, 60.

Gladiolus is one of the largest genera in the Iridaceae, comprising about 150 species. It is distributed from southern Europe, through the Mediterranean region into Africa. The majority of species occur in southern Africa with the greatest concentration in the winter rainfall region. The variation in the flower is considerable, ranging from actinomorphic to extremely zygomorphic species. It is one of the few in which the cytology has been intensively studied. Eleven species were examined by the present author, ten of which were found to have a diploid number of 30 (Table 12). The exception is *G. natalensis*, two varieties of which are polyploid and have chromosome numbers of 45, 60 and 75. The karyotypes are very uniform in all species, and the chromosomes are all small and acrocentric to submetacentric. The length of the chromosomes ranges from 1 to 2μ (fig. 22). The karyotype lacks distinguishing characteristics so that the diploid number and general size of the chromosomes are the only features of note. Satellites, which must be present, are seldom observed, and cannot be ascribed to any particular chromosome pair.

TABLE 13

Chromosome Numbers in *Acidanthera, Radinosiphon Homoglossum* and *Anomalesia.*

Species	Diploid No.	Collection Data or Reference
ACIDANTHERA		
A. bicolor Hochst	30	East Africa (ex hort) *Goldblatt 10* (J)
	30	(Sharma and Talukdar 1960)
A. aequinoctialis Bak.	30	Kanabali, Sierra Leone (Harvey 1966)
HOMOGLOSSUM Salisb.		
H. merianellum (L.) Bak. . . .	30	Silvermine Plateau, C.P. *Goldblatt 389*
H. watsonium (Thunb.) B.N.E.Br.	30	C.P. (ex hort) *Goldblatt 17* (J)
(as Gladiolus)	30	(Bamford 1941)
(as Gladiolus)	66	(Sharma & Talukdar 1966)
H. priori N.E. Br.	30	Fish Hoek, C.P. *Goldblatt 495*
H. abbreviatus (Andr.) Goldblatt	30	Botrivier, C.P. *Goldblatt 292*
RADINOSIPHON N.E. Br.		
R. cf. leptostachya N.E. Br. . .	30	Chimanimani Mountains, Rhodesia
(only seed & corms seen)		(raised from seed, flowers not seen)
R. leptostachya N.E. Br. . . .	30	Mt. Anderson, Tvl. *Goldblatt 600*
ANOMALESIA N.E. Br.		
A. cunonia (L.) N.E. Br. . . .	30	Glencairn, C.P. *Goldblatt 481*

All localities are in South Africa unless otherwise stated. Cape Province is abbreviated—C.P. Unless stated to the contrary all specimens are located in the Bolus Herbarium, Cape Town.

Two varieties of the summer rainfall area species, *G. natalensis* (*G. psittacinus*) were examined (fig. 22: J, K). In both cases wild populations were studied and were found to be cytologically heterogeneous. Multiples of 15 chromosomes were observed, ranging from 45 (triploid) to 75 (pentaploid). No diploid individuals were found.

As already mentioned, the cytology of *Gladiolus* has been quite extensively investigated. The results of a number of studies in this field were reviewed by Bamford (1935), who supplemented the existing work with many new chromosome counts (Bamford 1935; 1941).

From the approximately forty species studied by that date, both by Bamford and earlier workers, the following conclusions emerged. The basic number in the genus is 15 and the majority of species are diploid. As a whole the genus is heteroploid with somatic numbers ranging in multiples of 15 from 30 to 120 and higher. When arranged according to their geographical distribution, an interesting pattern emerged from the cytology of the species studied. The species occurring in the winter rainfall area of South Africa are all diploid (2n = 30). The tropical and southern African species of the summer rainfall area range from diploid through to hexaploid (2n = 90), while the European and Asian species are all high polyploids with somatic numbers of up to 180 having been recorded.

Unaware of Bamford's work, Mensinkai (1939) proposed an alternative interpretation of the cytology of *Gladiolus*. He found somatic numbers of 30, 60 and 80 in the few species he studied. On the basis of this and a meiotic study in which some irregularities were observed, he postulated that the basic number in *Gladiolus* was 10 and that species having a somatic number of 30 were triploid. In the light of present knowledge this interpretation must be disregarded.

The few cytological observations published after 1941 (fide Hamilton 1968) and the work of the present author confirm Bamford's conclusions. The six winter rainfall species studied here are diploid. Of these, the counts for *G. pritzellii*, *G. queizii*, *G. buckerveldii* and *G. ceresianus* are new records while those for *G. undulatus* and *G. brevifolius* confirm earlier findings. Five summer rainfall species were studied and as expected both diploid and polyploid species were found. Of the four which are diploid, namely *G. edulis*, *G. varius*, *G. praelongitubus* and *G. crassifolius*, the first three are new records and the last, that of *G. crassifolius*, confirms an earlier report. The counts for *G. natalensis* also confirm previous reports of its polyploid nature.

The position of *Gladiolus buckerveldii*.

This species, originally referred to *Antholyza*, then transferred to *Petamenes* by N. E. Brown, has been placed in *Gladiolus* by the present author. The grounds for this name change are dealt with fully in the discussion of the genera *Homoglossum* and *Petamenes*, and the taxonomic treatment is presented in a separate chapter dealing with all the name changes.

Heteroploidy in some species of *Gladiolus*.

One interesting feature which has emerged from the more recent studies is that several species appear to be heteroploid. Reports for *G. byzantinus* and *G. illyricus* give somatic numbers of both 60 and 90, and numbers of 120 and ±171 are recorded for *G. segetum*. Previous reports for *G. natalensis* (as *G. psittacinus*) were 2n = 90 (Bamford 1935), in which the present author found somatic numbers of 45, 60 and 75 in single wild populations of two varieties of this species.

Apomixis seems to be unlikely, for *G. natalensis* is reported to hybridise easily with other species and is believed to be one of the ancestors of the cultivated forms of *Gladiolus* which are usually tetraploid. A reduction in fertility would be expected in the triploid and pentaploid individuals due to meiotic abnormalities and this has been observed in many of the cultivated plants of *G. natalensis*. The occurrence of triploid individuals is remarkable as it suggests the presence of diploid plants which presumably hybridised with a tetraploid to yield the triploids. Diploid members of this species have, however, yet to be discovered, but a search for these may be rewarding. Another explanation of the presence of triploids and pentaploids is as follows. Populations may usually be either hexaploid or tetraploid, but where these two groups overlap in distribution, hybridisation would result in pentaploid plants. Abnormal meiosis would occur in these and could conceivably result in the production of haploid gametes. These when hybridised with a tetraploid could also produce the triploid individuals that were observed. It is, however, clear that populations of *G. natalensis* require further study and should produce interesting results.

The origin of *Gladiolus*

The occurrence of an increase in ploidy with distance from the Cape winter rainfall area seems to indicate a southern origin for the genus *Gladiolus* for it is clear that the diploid species could not be derived from the more northern polyploids. This hypothesis, which does not seem to have been mentioned previously, is supported by the occurrence of what are regarded as the most primitive species in the genus, with actinomorphic flowers, growing only in the south western Cape Province (Lewis 1954). The majority of species of *Gladiolus* have zygomorphic flowers and are thus regarded as more specialised.

It must be noted, however, that some diploid species of *Gladiolus* and related genera occur even north of the equator and could have given rise to the diploid species in the Cape Province. If this is correct then the actinomorphic species may not be primitive but specialised. The theory of the southern origin of *Gladiolus* seems the more acceptable.

The ancestry of *Gladiolus*

Geissorhiza has been proposed as the ancestor of *Gladiolus* (Lewis 1954). The reasons for this suggestion are the similarities between the least specialised species of *Gladiolus* and *Geissorhiza*. The woody, split, overlapping tunics of *Geissorhiza* occur in many species of *Gladiolus*, notably the least specialised amongst which are the actinomorphic species *Gladiolus stellatus*, *G. tenellus*, *G. quadrangulus* and *G. citrinus*. These species are recognised as belonging to

Gladiolus mainly by their winged seeds, these being globose in *Geissorhiza*, but in other respects the similarities are such that some authors have placed *Gladiolus stellatus* and *G. quadrangulus* in *Geissorhiza*.

The difference in the karyotypes of the two genera, *Gladiolus* having 15 and *Geissorhiza* 13 as the basic number, indicates that the relationship is not as close as the morphological evidence indicates. If the ancestral position of *Geissorhiza* is correct, *Gladiolus* would have had to originate by a process of increasing aneuploidy. The intermediate basic number of 14 has not been found in either genus but a study of the actinomorphic *Gladiolus* species not yet examined may provide the link. It must be noted that attempted crosses between the two genera made by the present author did not succeed (Table 1) and it is likely that *Gladiolus* and *Geissorhiza* have diverged to such an extent (assuming Lewis' suggested ancestry of *Gladiolus*) that they are no longer compatible. Again, hybrids between the actinomorphic species of *Gladiolus* and *Geissorhiza* may prove the exception and crosses between these should be attempted if possible.

ACIDANTHERA

$2n = 30$.

One species of this small tropical African genus, which is allied to *Gladiolus*, was studied here. It differs from most species of *Gladiolus* in having subequal perianth segments and broad, rather soft textured leaves. The diploid number is 30 and the karyotype is very similar to that of the diploid species of *Gladiolus*.

Two species of *Acidanthera* have previously been cytologically studied (Table 13), both having $2n = 30$, thus the count for *A. bicolor* by the present author is confirmatory (fig. 23: G). The karyotype of this species is very similar to that of the diploid species of *Gladiolus* (fig. 22). This similarity is significant because *Acidanthera* is a genus of rather doubtful validity.

The genus *Acidanthera* was based on the tropical species, *A. bicolor* described by Hochstetter (1845). Baker (1896), however, considered the genus widespread throughout Africa and included in it several discordant elements. Baker's misinterpretation was corrected by Lewis (1941) when she transferred the South African species to *Gladiolus*, *Engysiphon* or *Tritonia*. The tropical African species, which most resemble the type species, are all similar to *Gladiolus*. *Acidanthera* (sensu stricto) is distinguished from the tropical African species of *Gladiolus* by the nature of the perianth segments which are subequal in *Acidanthera* but unequal with the lower segments small and the posterior segment larger and hoodlike in *Gladiolus* (Baker 1896). The distinction does not hold when South African species of *Gladiolus* are taken into consideration because several species have a flower like *A. bicolor*, e.g. *G. tristis*, *G. undulatus* etc.

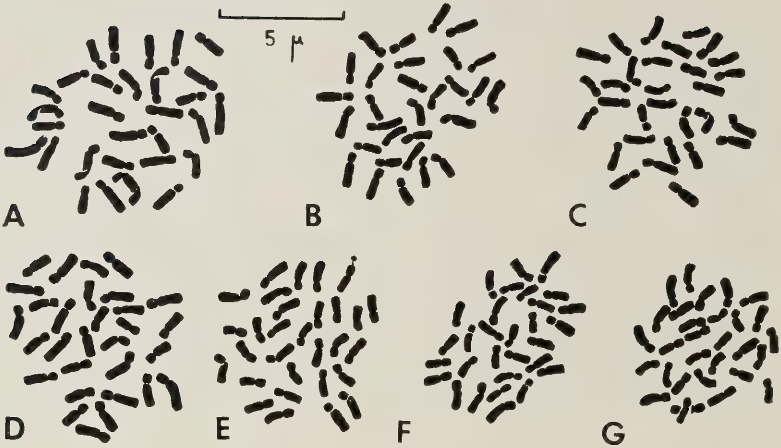

Fig. 23.
Karyotypes of *Homoglossum* (including *Petamenes*), *Acidanthera*, *Radinosiphon* and *Anomalesia*. A. *Homoglossum priori;* B. *H. watsonium;* C. *H. merianellum;* D. *H. abbreviatus;* E. *Anomalesia cunonia;* F. *Radinosiphon leptostachya;* G. *Acidanthera bicolor.*

The fact that species of *Acidanthera* and *Gladiolus* have been crossed successfully confirms the morphological and cytological evidence of the close relationship of the two. There are several records of *Gladiolus-Acidanthera* hybrids (Hamilton 1968; Wright 1966) and these "Gladanthera" hybrids are becoming known in horticulture.

As the evidence shows that there are neither morphological nor cytological grounds for maintaining *Acidanthera*, this genus must be incorporated in *Gladiolus*. In spite of this decision, the author recognised *Acidanthera* provisionally, and has refrained from making the necessary name changes until the genus as a whole can be dealt with.

RADINOSIPHON

2n = 30.

Radinosiphon is a small, rather poorly understood genus occurring mainly in the eastern mountains of southern Africa. A diploid number of 30 was obtained in *R. leptostachya*, the one species studied here. The karyotype resembles that of a diploid *Gladiolus*, having rather uniform small acrocentric chromosomes (fig. 23: F).

The diploid number in this genus, described here for the first time, is 30. The karyotype consisting of small, uniform chromosomes points strongly to a close relationship with *Gladiolus*. *Radinosiphon* was believed by Lewis (1954) to be allied to *Gladiolus*. Species of *Radinosiphon* broadly resemble a *Gladiolus*, but its flowers are rather small and the perianth segments subequal. Unlike most species of *Gladiolus* and its allies, it does not have winged seeds. This feature is however shared by some of the European species of *Gladiolus*.

The cytological evidence confirms Lewis' suggestion that the genus is allied to *Gladiolus* but little more can be said of the nature of the relationship. The genus clearly requires further morphological and cytological study before any conclusions can be drawn. Attempts to raise intergeneric hybrids between *Radinosiphon* and *Gladiolus* may also provide valuable information determining their relationship.

HOMOGLOSSUM, PETAMENES (now included in *Homoglossum*), *OENOSTACHYS ANOMALESIA, KENTROSIPHON*, (now referred to *Anomalesia*).

$2n = 30$.

These five genera are all allied to *Gladiolus* and can conveniently be discussed together. Although not all authors consider these genera to form a natural group with *Gladiolus*, evidence will be led to indicate that these comprise a single entity. The genera are all distinguished from *Gladiolus* and one another by various modifications of the perianth segments. The flowers become increasingly zygomorphic and tend to hide the natural affinities of these genera.

Cytology

Three of the approximately twelve species of *Homoglossum*, two of about eight species previously regarded as *Petamenes*, and one of the three species of *Anomalesia* were studied. All were found to have a similar karyotype in which the diploid number is 30 (Table 13). As in species of *Gladiolus*, *the* karyotype is undistinguished and consists of small acrocentric chromosomes which range in size from 1—2μ (fig. 23: A—E).

There have been only two previous chromosome counts in this group of genera, both for *H. watsonium* but published as Gladiolus, by Bamford (1941) who reported a diploid number of 30 while Sharma and Tulakdar (1960) found a somatic number of 66 in three cultivated forms of the plant they referred to *G. watsonius*. The count for *H. watsonium* by the present author confirms Bamford's finding. The counts for the other three species reported here are new records and indicate that the diploid number for *Homoglossum* is 30. It appears in the light of present results that the plant which Sharma and Talukdar investigated must have been misindentified. The counts for the species previously placed in *Petamenes* and for *Anomalesia* are new cytological records.

Intergeneric hybridisation

The genera under discussion are one of the few groups in the Iridaceae in which intergeneric hybrids can easily be produced. Hybrids between *Gladiolus* and *Homoglossum* are well known. Crosses between *G. tristis* and *H. watsonium* have been recorded by Bamford (1941) and recently by Ingram (1967). This hybrid which is known by the name "Homoglad" is fertile and produces fertile, vigorous offspring. The same cross has been made by the present author. Many amateur gardeners have made crosses between these two genera including Loubser (personal communication) who has reported that he has crossed several other species of *Homoglossum* and *Gladiolus*. There are also several records of natural hybrids occurring between *G. maculatus* and *H. watsonium*, which flower at the same time and in the same locality (Marloth 1915; *Judd sn.* BOL 30675).

Hybrids have also been produced between *Gladiolus* and *Anomalesia*, between *Gladiolus* and *Petamenes* (sensu lato) and between *Anomalesia* and *Kentrosiphon* (Table 1). Thus the genera appear to be interfertile amongst themselves as well as with *Gladiolus*.

Although not all the possible intergeneric crosses in this group have been made, the evidence strongly suggests that these will prove successful. At present the evidence is sufficiently strong to point to a close relationship among all the genera in this group. Likewise, those species which have been examined cytologically all exhibit a similar karyotype, another indication of close relationship. It is unfortunate that more species could not be found for cytological investigation, particularly among the several tropical African species of *Petamenes* now regarded as *Oenostachys*, the two recognised species of *Oenostachys* and *Anomalesia saccata*, previously the monotypic *Kentrosiphon*. The cytology of the last mentioned species is unknown, and only their morphological features have been used to determine their relationships.

Morphology

In the five genera under discussion there is a trend towards an increasing modification of the flower. In the least modified genus, *Homoglossum*, the perianth segments can be subequal but there is a tendency for an increase in the size of the uppermost segments in some species. In this genus the most modified species appears to be *H. vandermerwei* where the upper segment is the longest, and the three lower very much smaller than the upper ones (fig. 24: G). All the

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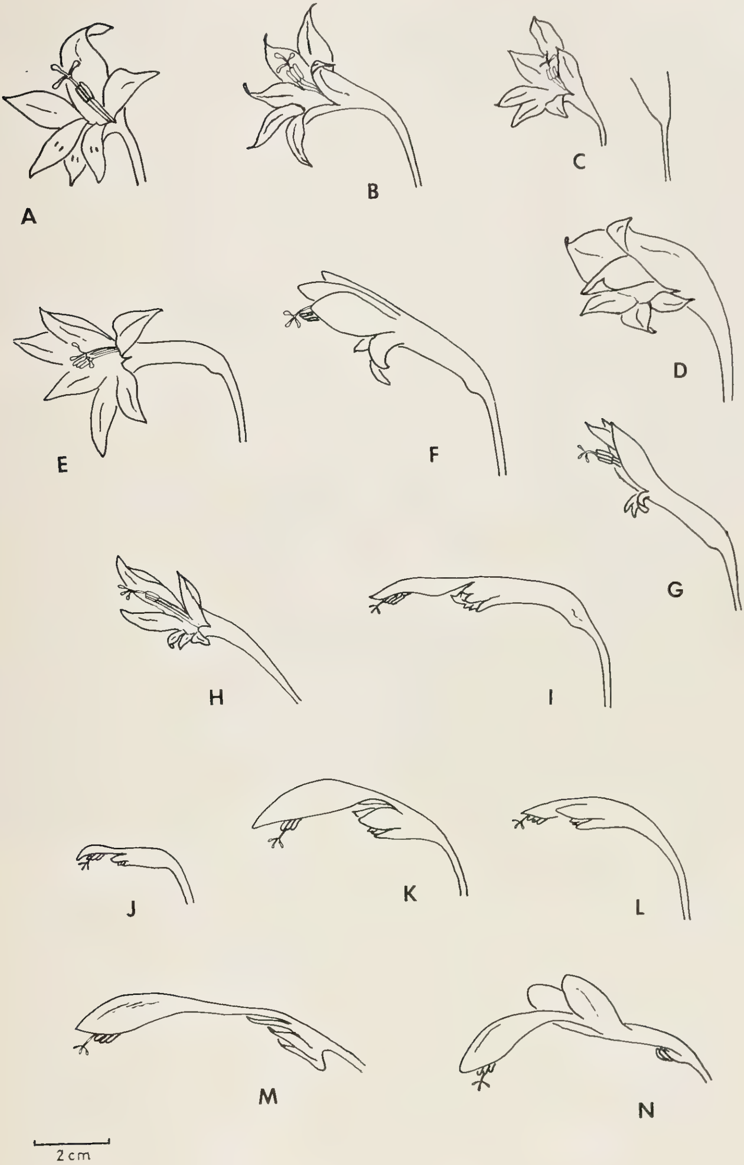
FIG. 24.

Flower structure in *Gladiolus* and its allies. A. *Gladiolus blandus;* B. *G. tristis;* C. *G. aureus;* D. *G. dracocephalus;* E. *Homoglossum watsonium;* F. *H. guthrei;* G. *H. vandermerwei;* H. *Gladiolus buckerveldii;* I. *Homoglossum abbreviatus;* J. *Oenostachys vaginifer;* K. *O. zambeziaca;* L. *O. dichroa;* M. *Anomalesia saccata* (*Kentrosiphon*); N. *A. cunonia.*


A
B
C
D
E
F
G
H
I
J
K
L
M
N
2 cm

species in this genus have a similar perianth tube, narrow at the base, widening abruptly into a wider tubular portion and usually bearing a small sac on the abaxial side of the tube at the point where the perianth tube narrows. This sac is unfortunately not well developed in some species, e.g. *H. priori*, making identification difficult. This type of perianth is not found in *Gladiolus* (fig. 24: A—C) for although *G. aureus* has a similar tube with a rather abrupt constriction, it has no sac, and the upper portion is not tubular but widens progressively. Thus *Homoglossum* can always be distinguished from *Gladiolus* on the morphology of the perianth tube, although the flower of some species can otherwise easily be confused with *Homoglossum*.

Homoglossum abbreviatus (*Petamenes*) has the same type of perianth tube as other species of *Homoglossum*, but here the upper perianth segment is far larger than the others (fig. 24: I) and constitutes the diagnostic feature for the genus.

The flower modification in this species is of the same nature as in *Homoglossum* and differs merely in degree, the uppermost perianth segment being well developed. This difference is clearly one of degree and this together with their very similar vegetative characters prompted Bolus (1933) to write that *Petamenes abbreviatus* barely escaped being placed in *Homoglossum*.

The vegetative features shared by *Homoglossum* and *P. abbreviatus* are a small corm and a single slender, linear leaf with pronounced margins. These vegetative features bear a strong resemblance to those found in many species of *Gladiolus*, amongst others *G. tristis* and *G. liliaceus*, which constitute a natural group within that genus. The other type of vegetative form found in *Gladiolus* species such as *G. natalensis* and *G. floribundus*, also indicative of a natural grouping, consists of a larger corm and several rather broad, ensiform leaves.

The other South African species of *Petamenes*, *P. buckerveldii* (now treated as *Gladiolus*) has this latter vegetative form and is rather different from *P. abbreviatus* in having a tapering perianth tube (fig. 24: I) which widens gradually and lacks the sac found in *P. abbreviatus*. The perianth segments are also less modified so that the upper segment is not much larger than the others. In fact, this type of perianth tube and flower are very similar to those found in some species of *Gladiolus*. Its vegetative features, which differ from *P. abbreviatus*, indicate that it is misplaced in its present genus and it has accordingly been transferred to *Gladiolus*, probably a far more natural position for this species where its only slightly modified flower would not be out of place.

The remaining species of *Petamenes* are found in tropical and southern Africa and appear to form a natural unit. Most species have a large corm and several relatively broad, ensiform leaves. The flowers have a long perianth tube which is narrow at the base and broadens to form a wide throat. The widening is not, however, abrupt and there is no sac as found in *Homoglossum* and

Petamenes abbreviatus. The upper perianth segment is much enlarged and hood-like, the two upper lateral segments are far smaller and the lower segments even smaller (fig. 24: K, L).

The two species of *Oenostachys* have a similar vegetative form and flower (fig. 24: L) and differ only in having unusually large bracts. *Oenostachys dichroa* is also reported to have bifid stigmas, but this feature is probably not significant in this case for, as the author has pointed out in a previous section, bifid stigmas occur randomly throughout the tribe *Ixieae* and probably do not have the taxonomic importance once accorded them. It is more likely that this plant has the usual bilobed stigmas of most species of *Gladiolus* and allies but with a more pronounced cleft.

Kentrosiphon and *Anomalesia* also have large corms and several fairly broad leaves but have the most modified flowers in the group (fig. 24: M, N). In both, the perianth tube is short and narrow and the uppermost segment is extremely large and hooded. The three lower segments are small and are bent upwards forming a sac-like structure. In *Anomalesia* the two upper lateral segments are large and form reflexed wings, while in *Kentrosiphon* these segments are smaller and form, with the lower segment, a part of the sac at the mouth of the perianth tube. In this genus the sac is more strongly developed and has a small spur extending backwards.

Taxonomic history

Many species in the five genera discussed in this section have at some period been regarded as allied to *Gladiolus*. The type species of *Petamenes* and of Homoglossum were originally described as species of *Gladiolus* and the type species of *Anomalesia* was at one time transferred to *Gladiolus*, having first been described as a species of *Antholyza*. Baker (1896) placed all the species of the group in *Antholyza*. In his expanded concept of this genus, Baker included not only the zygomorphic allies of *Gladiolus*, but species unrelated to these like *Antholyza ringens*, an ally of *Babiana*, and *Curtonus paniculatus*, regarded by the present author as a *Crocosmia*.

The basis for the genus *Antholyza* as understood by Baker was the medianly zygomorphic flower with a long perianth tube, this being peculiar in having a narrow basal portion which widened rather abruptly into a wide tubular upper part. Many of the species included in this group also had a rather large expanded upper perianth segment, often hood-like.

This unnatural assemblage was revised by N. E. Brown (1932) but prior to this the genus *Oenostachys* containing a single species with vegetative features and a flower exactly like the tropical African species of *Antholyza* was described by Bullock (1930). The species was not placed in *Antholyza* mainly because of its very large wine coloured bracts which completely enveloped the flowers and its bifid stigmas.

Brown continued the fragmentation of *Antholyza*, recognising *Oenostachys* and adding another species to this genus. Out of *Antholyza* (sensu Baker) Brown recognised ten genera; *Petamenes* and *Homoglossum* were revived, having originally been described by Salisbury; *Antholyza* was left as a monotypic genus; and six new genera were created. This treatment was more satisfactory than Baker's concept but proved a little unwieldy owing to the large number of genera that were recognised, many being monotypic or containing very few species. Brown's treatment has been altered slightly by later workers who sought to simplify it and to decrease the number of genera.

The first of these was Hutchinson (1934) who, in his classification of the Iridaceae, recognised the tribe *Antholyzeae* containing all but one of the genera originally placed in Baker's genus *Antholyza*, the exception being *Oenostachys* which was placed in the same tribe as *Gladiolus*. Hutchinson recognised all but one of Brown's genera, merging *Chasmanthe* and *Petamenes*. In view of the cytological evidence (see chapter on *Tritonia* and its allies) *Chasmanthe* having 20 somatic chromosomes and *Petamenes* 30, the value of this step must be regarded with doubt. The tribe *Antholyzeae* as constituted by Hutchinson is no more natural than Baker's genus, for it still contains disparate elements similar only in flower structure.

Phillips (1941) modified Brown's treatment further, as he incorporated *Anomalesia* and *Kentrosiphon* together with the probably unrelated *Chasmanthe* in *Petamenes*, a grouping he recognised as having the upper perianth segment large and hooded. Apart from the inclusion of species of *Chasmanthe*, Phillips' step has its merits for it reduced the number of genera and attempted to maintain the natural groupings. The modifications made by Hutchinson and Phillips were not followed by taxonomists and Lewis (1954) continued to recognise all of Brown's genera though she suggested the incorporation of *Kentrosiphon* in *Anomalesia*.

Lewis pointed out the diverse nature of the old genus *Antholyza* and grouped the genera created from it in more natural positions, placing, for example, *Chasmanthe* near *Crocosmia* and *Curtonus*, and *Antholyza* near *Babiana* (see relevant chapters). In doing so she placed less emphasis on floral morphology and took vegetative features into account. Lewis recognised two independent lines of evolution from *Gladiolus*, one leading to *Anomalesia* (including *Kentrosiphon*) and the other to *Homoglossum* and *Petamenes*. This treatment certainly seems the most natural, for though the floral modifications are similar, the first group has several broad leaves and the second only one or two linear leaves.

A proposed rearrangement of the genera

It is with some misgiving that the present author undertakes a re-evaluation of the status of this group of genera, once classified in the genus *Antholyza*.

That they do constitute a natural group is now quite clear for not only do they resemble different species of *Gladiolus* in their vegetative characteristics but appear from the evidence of breeding experiments and cytological study to form a potentially interfertile complex.

The close study of the kind of modification occurring in the flower together with the vegetative features indicates that there are two separate evolutionary lines and that in both a similar trend has occurred leading to increasingly zygomorphic flowers. All the genera are very closely allied to *Gladiolus*, and an argument can be made for their inclusion in that genus. This is particularly true of the less specialised species. As *Gladiolus* is itself a very large and already unwieldy genus of about 150 species this step would certainly not be advisable. It is thus proposed to treat the group in as natural a manner as possible and to arrange it in as convenient a system as can be devised. The question of convenience is an awkward one for it is difficult to know what will cause least difficulty. The following system is proposed.

Homoglossum

The genus *Homoglossum* is maintained and expanded to include *Petamenes abbreviatus* which is naturally allied to this genus. In its revised form *Homoglossum* now includes those plants with subequal or unequal perianth segments where the upper segment is enlarged to form a hood. In all species the perianth tube consists of a narrow basal and abruptly widened upper portion with a small sac at the junction of the wide and narrow parts. The vegetative form in this genus consists of a small corm and a few slender leaves, usually only one. As already pointed out, *Homoglossum* would be a genus of convenience, and should be recognised only if it continues to be such. The somewhat arbitrary difference between *Homoglossum* and *Gladiolus* may necessitate several changes in nomenclature later.

Oenostachys

As already mentioned, *Petamenes buckerveldii* does not really belong to the genus *Petamenes* and it has been transferred to *Gladiolus* where its only slightly modified flower is not unusual. The remaining species of *Petamenes* should be transferred to *Oenostachys*. The flower in these species is modified in the same way as in *Homoglossum* with a hood-like upper segment but has a perianth tube with a tapering upper portion and is without a sac. The vegetative form is similar in most species and consists of a large corm and several broad ensiform leaves. The major difference is in the size of the bracts which are largest in *O. dichroa*, smaller in *O. abbreviatus* which forms a link between *O. dichroa* and the remainder of the group which have smaller bracts.

Anomalesia

Finally, *Kentrosiphon* is incorporated in *Anomalesia*. The idea that these two genera should be combined is not new, for Klatt (1882) placed both in his new but nomenclaturally invalid genus *Anisanthus*. Lewis (1954) also suggested that they be merged. Although the flowers are rather different in appearance they are modified in a similar way. The perianth tube is narrow and short and the lower segments form a sac-like structure at the mouth of the tube. The vegetative features are similar and like most species in the previous group, the species have large corms and several relatively broad ensiform leaves.

Conclusion

The genus *Gladiolus* and its allies, however circumscribed, form one single group of genera sharing a number of morphological features, a similar karyotype and can in many instances be crossed. These genera should be placed in subtribe *Gladiolineae*. The genera recognised by the present author in this subtribe are *Gladiolus*, *Radinosiphon*, *Homoglosusm*, *Oenostachys* and *Anomalesia*.

f. Subtribe *Ixiineae*

Dierama, Ixia, Sparaxis, Synnotia

This group comprises herbaceous plants with both evergreen and deciduous aerial leaves. All representatives have a corm, covered with reticulate fibres and in general have fairly unspecialised flowers, the exception being *Synnotia* where some species are very zygomorphic. The bracts are generally dry and membranous and the style branches short and undivided.

DIERAMA

$2n = 20.$

There are about twenty species in this genus, distributed along the mountainous regions of Africa from Ethiopia to the eastern Cape. The plants are comparatively large for the tribe *Ixieae* and are unusual in that many species are evergreen. *Dierama* is characterised by having a tall, branched scape with pendulous spikes of large actinomorphic, short-tubed flowers. A very characteristic feature of the genus is the large, dry, scarious bracts.

The five species examined here (Table 14) all have a similar karyotype in which the diploid number is 20 (fig. 25: A—E). The chromosomes range from 1,5 to about 3μ long. The larger ones are acrocentric and the smaller submetacentric. There are two pairs of chromosomes which are appreciably longer than the others and the second longest of these bears a satellite, though this is not always clearly seen. Occasionally a second satellite on a small chromosome is seen but as this is not clear it has not been included in the idiogram for *Dierama* based on the karyotype of *D. gracile*.

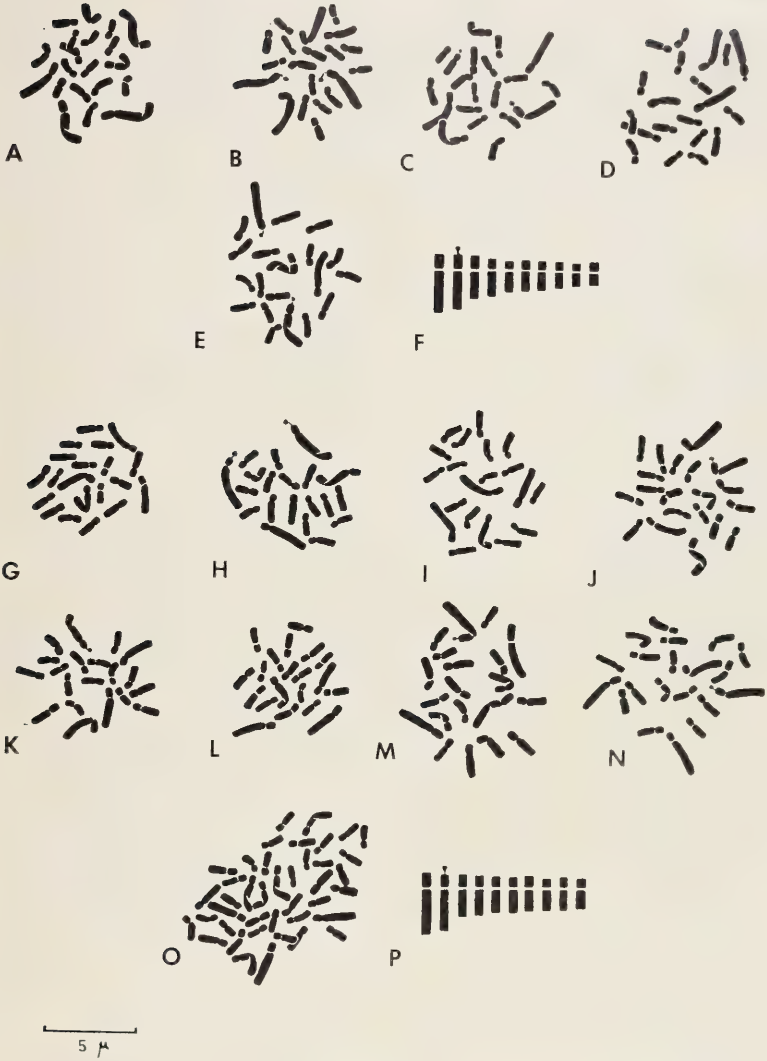


FIG. 25.

Karyotypes and idiograms of *Dierama* and *Ixia*. A. *Dierama galpinii;* B. *D. gracile;* C. *D. reynoldsii;* D. *D. medium aff.;* E. *D. luteo-albidum;* F. Idiogram of *Dierama;* G. *Ixia rapunculoides;* H. *I. odorata;* I. *I. longituba;* J. *I. erubescens;* K. *I. scillaris;* L. *I. flexuosa;* M. *I. dubia;* N. *I. polystachya;* O. *I. orientalis;* P. Idiogram of *Ixia.*

Only one species of Dierama has previously been studied cytologically, namely *D. pendulum* by Vilmorin & Simonet (1927) who found 2n = 20, a count confirmed by Goldblatt (1969). With a total of six of the twenty species in this genus having been reported as having a similar karyotype with a diploid number of 20, it is assumed that the basic number in the genus is 10.

TABLE 14
Chromosome numbers in *Dierama, Ixia, Sparaxis* and *Synnotia.*

Species	Diploid No.	Collection Data or Reference
DIERAMA C. Koch		
D. pendulum (L.f.) Koch	20	Vilmorin & Simonet 1921; Goldblatt 1969.
D. galpinii N.E. Br.	20	Saddleback, Barberton, Tvl. *Goldblatt 21* (J)
D. gracile N.E. Br.	20	Haenertsburg, Tvl. *Goldblatt 59* (J)
D. reynoldsii Verdoorn	20	Bergville, Natal. *Goldblatt 162* (J)
D. medium N.E. Br.	20	Wolkberg, Tvl. *Goldblatt 153* (J)
D. luteo-albidum Verdoorn	20	Lions River, Natal. *Davidson s.n.* (J)
IXIA L.		
I. campanulata Houtt. (as I. crateriodes)	20	(Brittingham 1934)
I. viridiflora Lam.	20	(Collins, fide Darlington & Wylie 1955)
	20	(Goldblatt 1969)
I. ranunculoides Delile	20	Nieuwoudtville, C.P. *Goldblatt 159* (J)
I. odorata Ker.	20	Malmesbury, C.P. *Goldblatt 505*
I. longituba N.E. Br.	20	Riversonderend, C.P. *Goldblatt 452*
I. erubescens Goldblatt (=I. crispa)	20	Tulbagh Road, C.P. *Goldblatt 202*
I. scillaris L.	20	Pakhuis Pass, C.P. *Goldblatt 104*
I. flexuosa L.	20	Quoin Point, C.P. *Goldblattt 332*
I. dubia Vent.	20	Kalk Bay Mountains, C.P. *Goldblatt 325*
I. polystachya L.	20	Table Mountain, Cape Town, C.P. *Goldblatt 377*
	20	(Fernandes & Neves 1961)
(as I. leucantha)	20	(Fernandes & Neves 1961)
I. orientalis L. Bol.	40	Hogsback, C.P. *Goldblatt 391*
SPARAXIS Ker		
S. tricolor (Schneev.) Ker.	20	Nieuwoudtville, C.P. *Goldblatt 137* (J)
	20	(Brittingham 1934)
	20	(Nakajima, fide Darlington & Wylie 1955)
S. elegans (Sweet) Goldblatt	20	Nieuwoudtville, C.P. (Goldblatt 1969)
S. bulbifera (L.) Ker	20	Ysterplaat, Cape Town, C.P. *Goldblatt 262*
S. pillansii L. Bol.	20	Nieuwoudtville, C.P. *Goldblatt 327*
S. fragrans (Jacq.) Ker	20	Botrivier, C.P. *Goldblatt 296*
S. grandiflora subsp. fimbriata (Lam.) Goldblatt	20	Signal Hill, C.P. *Goldblatt 265*
subsp. acutiloba Goldblatt	20	Clanwilliam, C.P. (Goldblatt 1969)
SYNNOTIA Sweet		
S. villosa (Burm. f.) N.E. Br.	20	Hopefield, C.P. *Goldblatt*
S. galeata (Jacq.) Ker	20	Van Rhyns Pass, C.P. *Goldblatt*
S. variegata Sweet	20	Clanwilliam, C.P. (Goldblatt 1969)

All localities are in South Africa. The provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Unless otherwise stated all specimens are housed at the Bolus Herbarium Cape Town.

IXIA

Ixia is believed to be a derivative of *Dierama* and is found mainly in the winter rainfall region of the Cape Province. The plants are smaller than *Dierama*, and the aerial parts are deciduous. The flowers are generally smaller, not pendulous, and have smaller membranous bracts.

There are forty-four species recognised in this genus, nine of which were examined here. In all but one, the diploid number is 20. The odd one, *Ixia orientalis* has $2n = 40$, and appears to be a polyploid species (fig. 25: G—P). The chromosomes range from 1,5 to 3,3μ and are acrocentric, though the smaller ones tend to be submetacentric. There are two pairs of longer chromosomes and the shorter of these bears a satellite. As the karyotypes of all the species examined are similar, the idiogram, based on *I. dubia* can be regarded as representative of the genus. A comparison of the idiograms of *Dierama* and *Ixia* shows the great similarity between these two genera.

Prior to this work, three named species of *Ixia* had been studied cytologically (Table 14), a diploid number of 20 being reported for all three. In addition, different hybrids studied by Brittingham were found to be diploid and polyploid, having somatic chromosome numbers of 20 or 40. Of the nine species studied in this work, eight are new chromosome counts and the record for *I. polystachya* confirms the previous count of Fernandes & Neves.

The karyotype as described by Brittingham and Fernandes & Neves confirms the finding by the present author that it consists of two long pairs and eight short pairs of chromosomes. With a total of eleven of the forty-four species in the genus having now been studied, it can be suggested that the basic number for the genus is 10.

The occurrence of polyploidy in *I. orientalis* is unusual, as polyploids are not common in South African Iridaceae, particularly in the tribe *Ixieae*, although polyploid species have been found in *Romulea*, *Geissorhiza*, *Tritonia* and *Gladiolus*. Before it can be decided that *I. orientalis* is a consistently polyploid species, other populations should perhaps be examined. It is, however, interesting to note that *I. orientalis* occurs in the easternmost limit of the range of distribution of the genus, and it is the only species of *Ixia* in the summer rainfall area.

The subgenus *Dichone*

The subgenus *Dichone* of *Ixia* is a group of species which was transferred by Lewis (1962) from *Tritonia* to *Ixia*. Although species placed in *Dichone* were originally referred to *Ixia* they were considered by Klatt (1882) and Baker (1876) to belong to *Tritonia*, and remained in that genus until transferred by Lewis, who did so on purely morphological grounds.

The two species in this group which were studied here, namely *I. scillaris* and *I. crispa* were found to have a diploid number of 20 and karyotypes similar to those of other species of Ixia. *Tritonia* and its allies, however, have a rather different karyotype and a basic number of 11. Thus cytological evidence confirms the decision of Lewis to transfer this group to *Ixia.*

The relationship between *Ixia* and *Dierama*

Ixia and *Dierama* have very similar karyotypes (fig. 25). This is evidence of the close relationship of the two genera, and confirms the accepted view that *Dierama* merges into *Ixia* and that *Dierama* gave rise to *Ixia*. It has been suggested by Lewis (1962) and supported by Goldblatt (1969) that *Dierama* which has a wide distribution from tropical Africa to the eastern Cape Province is the more primitive genus, while *Ixia* which is limited to the southern and western Cape Province is derived from it. The reasons proposed for this view are that *Dierama* has a series of unspecialised features, e.g. evergreen habit, much branched inflorescence, large persistent corms and regular flowers with a short perianth tube. It is believed that *Ixia* evolved from *Dierama* in response to the more exacting ecological conditions in the western Cape Province, for *Ixia* has deciduous aerial leaves, a small short-lived corm, a brief growing season and reduced inflorescence with more specialised flowers, all of which are believed better suited to the long, dry, hot summer, the wet winter and short spring period.

SPARAXIS

$2n = 20.$

Sparaxis is a small genus comprising six species, occurring in the south-western Cape Province. The plants are small with erect, usually unbranched inflorescences of large brightly coloured, regular or sub-zygomorphic flowers. A characteristic feature of the genus is the large, dry, scarious and lacerated bracts, similar to those in *Dierama.*

Five of the six species of *Sparaxis* were studied in the present work (Table 14). All exhibit a constant and characteristic karyotype. The diploid number is 20 and the chromosomes are fairly small and acrocentric (fig. 26: A—E). There appear to be two pairs of longer chromosomes one bearing a satellite. The size range is from about 1,5 to 3μ. Thus the karyotype is similar to that of *Ixia* and *Dierama*, though all the chromosomes tend to be slightly smaller. The idiogram of the karyotype of *S. grandiflora* (fig. 26: F) can be regarded as representative of the genus.

Prior to this work, three species of *Sparaxis* had been cytologically investigated, all having a diploid number of 20. In the present study the remaining three species were investigated for the first time while the counts for *S. tricolor* and *S. grandiflora* subsp. *fimbriata* confirm previous reports for these two.

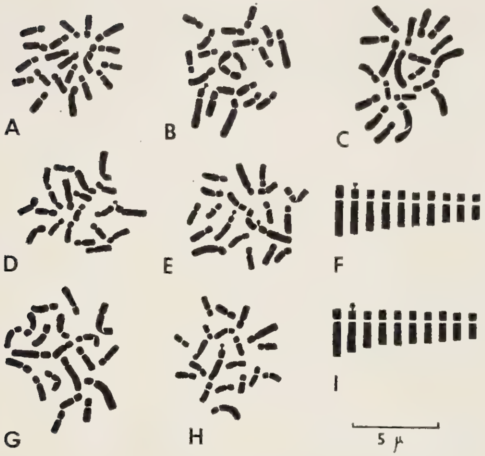


FIG. 26.

Karyotypes of *Sparaxis* and *Synnotia*. A. *Sparaxis tricolor;* B. *S. bulbifera;* C. *S. pillansii;* D. *S. fragrans;* E. *S. grandiflora* subsp. *fimbriata;* F. Idiogram of *Sparaxis;* G. *Synnotia villosa;* H. *S. galeata;* I. Idiogram of *Synnotia.*

As all the species in the genus have been studied it is clear that the basic number for the genus is 10. Brittingham (1934) and Goldblatt (1969) reported that the karyotypes of *Sparaxis* and *Ixia* are remarkably similar, an observation repeated in the present study, although the chromosomes of *Sparaxis* appear to be slightly smaller than those of *Ixia*. This similarity of karyotype may perhaps be regarded as evidence of phylogenetic relationship and will be discussed after the section on *Synnotia.*

SYNNOTIA

2n = 20.

Synnotia is another small genus occurring in the south western Cape. It is closely allied to *Sparaxis*, the plants differing only in having longer tubed, zygomorphic flowers.

Two of the five species in this small genus were examined cytologically (Table 14). The karyotypes of both are similar, and resemble *Sparaxis* closely. The diploid number is 20 and of the range of fairly small chromosomes, two pairs are conspicuous, being somewhat larger. The size of the chromosomes is the same as in *Sparaxis*. In only one of the longer chromosomes of *S. galeata* a satellite was seen while none were visible in *S. villosa*. However, this satellite has been included in the idiogram of the karyotype of *S. galeata* as it is suspected that the satellites are present even if not often clearly seen (fig. 26: I).

The first cytological record for this genus was that of Goldblatt (1969) who obtained a diploid number of 20 in *S. variegata*. It was also reported that the karyotype closely resembled those of *Sparaxis*, *Dierama* and *Ixia*. Two more species have been examined in this work with similar results. The karyotype of *Synnotia* resembles most closely that of *Sparaxis* in that the chromosomes are slightly smaller than in *Ixia* and *Dierama* (fig. 26: G—I).

A suggested phylogeny of *Sparaxis* and *Synnotia*

That *Dierama*, *Ixia*, *Sparaxis* and *Synnotia* form a natural group was suggested by Goldblatt (1969). These genera all have a basic number of 10 and have a karyotype unique in the Iridaceae. The relationship between *Dierama* and *Ixia* has already been discussed and it is believed that *Sparaxis* and *Synnotia* were derived from *Dierama* in a way similar to that described for *Ixia*.

Both *Sparaxis* and *Synnotia* are deciduous and have a short growing season. They are small in size and are modified to resist very dry conditions. Both have, however, some features in which they resemble the genus *Dierama* very closely; the bracts and bracteoles of the three genera are unusual in the Iridaceae, being firm, dry, scarious and often lacerated; the capsules are comparatively hard walled and contain seeds which are unusual in that they are round and very glossy.

It is believed by the present author that *Synnotia* was derived from *Sparaxis*. They share a large number of morphological features, a similar karyotype and, except for their flowers, cannot be distinguished. These genera appear to be interfertile and a bigeneric hybrid between *Sparaxis* and *Synnotia* has been obtained. The capsules were fully developed and the seed was viable (Goldblatt 1969). Though the hybrids have not yet flowered they are growing vigorously.

The taxonomic position of *Synnotia*

The morphological differences between *Sparaxis* and *Synnotia* are slight for they differ only in flower structure. The flowers of *Sparaxis* are actinomorphic or sub-zygomorphic and have a very short perianth tube, while in *Synnotia* the flowers are highly zygomorphic and have a comparatively long and in some species, curved perianth tube. The perianth segments in *Sparaxis* are subequal but in *Synnotia* the posterior segment is somewhat enlarged and in most species forms a hood. Thus, the difference between the genera is in the degree of modification of their flowers.

This situation has a parallel in *Gladiolus* and its allied genera *Homoglossum*, *Petamenes* and *Anomalesia*, where again the degree of floral modification separates the genera. It was suggested by the author that, for *Gladiolus* the unusual or extremely zygomorphic species be grouped in genera separate from *Gladiolus*, mainly for the sake of convenience. Although the degree of zygomorphy in *Synnotia* is perhaps not as extreme as in those genera allied to *Gladiolus*, it may be retained as a valid genus, again on grounds of convenience as well as minor morphological differences.

Intergeneric hybrids.

Apart from the already mentioned *Sparaxis x Synnotia* cross, no intergeneric hybrids were obtained in the four genera under discussion. The present author attempted crosses between *Dierama* and *Ixia* and between *Dierama* and *Sparaxis* (Table 1) but none was successful. This information can be taken as evidence that *Dierama*, *Ixia* and *Sparaxis* are quite distinct genera and if they are related, they have diverged sufficiently to exclude the possibility of any hybridisation taking place. As *Dierama* and *Ixia* are believed to merge into one another, more crosses should perhaps be attempted, particularly between the border-line species.

Conclusion

The relationship of the four genera, *Dierama*, *Ixia*, *Sparaxis* and *Synnotia* has often been regarded as fairly close and they have usually been placed in the same tribe or subtribe together with several other genera. Lewis (1954), who had a detailed knowledge of the South African Iridaceae, placed these four genera together with *Gladiolus* and its allies and *Tritonia* and allies in her subtribe *Ixiineae*. She states that attempts to divide the group into smaller units was difficult due to the great degree of morphological similarity. Hutchinson (1934) whose classification of the family was based mainly on flower structure, split the genera into tribes rather unnaturally resulting in *Dierama* and *Ixia* and *Streptanthera*, a genus incorporated in *Sparaxis* (Goldblatt 1969), being in a separate tribe from *Sparaxis* and *Synnotia*.

As has been shown in the present work the four genera under discussion share a number of morphological characteristics some of which are unique in the family, and appear to form a fairly natural group. These genera have been shown to have a similar and distinctive karyotype and have a basic chromosome number of 10 which confirms the evidence of morphological similarity. It is thus proposed that Lewis' subtribe *Ixiineae* be maintained, though in a modified form, to comprise only *Dierama*, *Ixia*, *Sparaxis* and *Synnotia*.

g. Subtribe ***Tritoniineae***

Crocosmia (including *Curtonus*), *Tritonia*, *Chasmanthe* and *Montbretiopsis*

This group of genera are generally small, herbaceous plants with spherical to flattened corms with tunics of fairly fine fibres. The slightly zygomorphic flowers are usually yellow or orange, although reds and pinks do occur.

CROCOSMIA

2n = 22.

This genus occurs in the summer rainfall area of south east Africa, usually in forested highland areas. The genus is distinguished by its squat capsule, each loculus containing only a few seeds. The monotypic genus *Curtonus* is treated here as part of *Crocosmia* and reasons for this are presented in the following text.

Five of the seven species in the genus and one hybrid were examined by the present author (Table 15). The diploid number is 22 in the representatives examined (fig. 27: A—G). The chromosomes are quite small, ranging from under 2 to just less than 3μ in length. Although there is a graduation in size, six pairs of somewhat longer chromosomes can be recognised and the karyotypes have no striking features. Satellites are seldom clearly seen though one or two are sometimes noticed on the longer chromosomes. Only in *C. aurea* were three seen. However, it is presumed that there are actually four satellites in the karyotype. Thus the idiogram of *C. aurea* is shown with two long chromosomes bearing satellites. One unusual feature noticed in *C. aurea*, *C. pottsii* and the hybrid is the presence of a single pair of metacentric chromosomes which serve to distinguish these species. In the remaining three species the preparations yielded rather smaller chromosomes and the metacentric chromosomes could not be recognised easily and are not drawn.

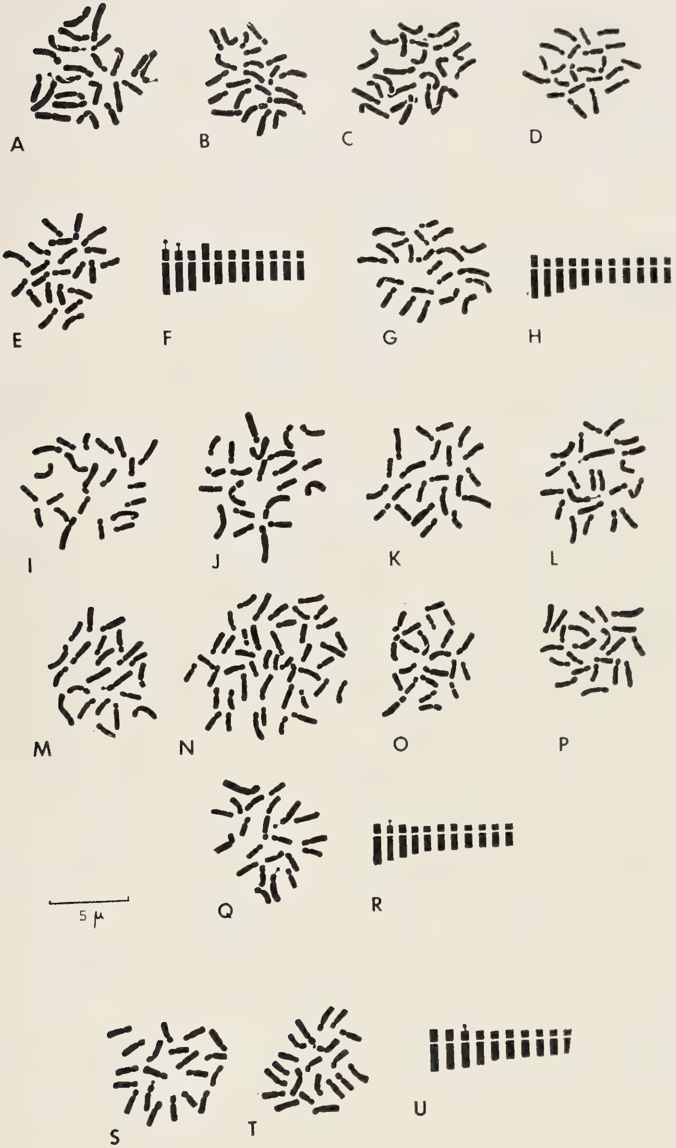
The present study confirms the previous counts for *C. aurea* and *C. pottsii* and also for the hybrid *C. x crocosmiiflora* (Table 15). In addition, *C. mathewsiana* and *C. masonorum* are reported here for the first time. As a diploid number of 22 has been recorded for the five species studied of the seven in the genus, it seems clear that the basic number in *Crocosmia* is 11.

Brittingham (1934) reported a chromosome number of 26 in *Antholyza paniculata*, a synonym of *Crocosmia paniculata*, studied here. There is little similarity between Brittingham's illustration and the karyotype described by the present author and it is suggested that Brittingham's count was not for this plant but some other species, the identity of which is unknown.

The plant known as *C. x crocosmiiflora* has long been regarded as a hybrid and it is, in fact, almost sterile for few seeds are ever produced. Both Ernst-Schwartzenbach (1930) and Brittingham (1934) postulated that it is a hybrid between *C. aurea* and *C. pottsii*. As far as the author is aware, this is only a suggestion and requires confirmation by actually repeating this cross.

FIG. 27.

Karyotypes and idiograms of *Crocosmia*, *Curtonus*, *Tritonia* and *Chasmanthe*. A. *Crocosmia aurea;* B. *C. pottsii*, C. *C. crocosmiiflora*, D. *C. masonorum*, E. *C. mathewsiana*, F. Idiogram of *C. durea;* G. *Crocosmia paniculata* (previously *Curtonus*); H. Idiogram of *C. paniculata;* I. *Tritonia moggii;* J. *T. coccinea;* K. *T. wilsonii;* L. *T. crispa;* M. *T. nelsonii;* N. *T. lineata;* O. *T. flabellifolia;* P. *T. deusta;* Q. *T. squalida;* R. Idiogram of *Tritonia;* S. *Chasmanthe aethiopica;* T. *C. floribunda;* U. Idiogram of *Chasmanthe*.


A
B
C
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E
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5 μ
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U

Table 15

Chromosome numbers in *Crocosmia*, *Tritonia* and *Chasmanthe*.

Species	Diploid No.	Collection Data or Reference
Crocosmia Planch		
C. aurea Planch	22	(Shibata, fide Index of Plants Chromosome Numbers, 1963)
	22	Woodbush, Haenertsburg, Tvl. *Goldblatt 11* (J)
C. pottsii (Bak.) N.E. Br.	22	(Ernst-Schwartzenbach 1930)
	22	(Nakajima, fide Darlington & Wylie 1955)
	22	Mooi River, Natal. *Goldblatt 98* (KJ)
C. × crocomiiflora (Nicholson) N.E. Br.	22	(Ernst-Schwartzenbach 1930)
	22	Brittingham 1934
	22	(Meurman & Suomalainen, fide Darlington and Wylie 1955)
	22	ex hort. *Goldblatt 516.*
C. masonorum (L. Bol.) N.E. Br.	22	ex hort. *Goldblatt 77* (J)
C. mathewsiana L. Bol.	22	Graskop, Tvl. *Goldblatt 417*
C. paniculata (Klatt) Goldblatt	22	Saddleback, Barberton, Tvl. *Goldblatt 61* (J)
(as Antholyza paniculata)	26	(Brittingham 1934)
Tritonia Ker		
T. crocata (L.) Ker	20	(Brittingham 1934)
	22, 60.	(Sharma and Sharma 1960)
T. deusta (Ait.) Ker	22	Stormsvlei, C.P. *Goldblatt 514*
T. squalida (Ait.) Ker	22	C.P. (ex hort) *Goldblatt 32* (J)
T. moggii Oberm.	22	Inhaca Island, Mozambique. *Goldblatt 2* (J)
T. coccinea L. Bol.	22	Port St. John, C.P. *Goldblatt 382*
T. wilsonii Bak.	22	Fort Hare, C.P. *Goldblatt 406.*
T. crispa (L.f.) Ker	22	Giftberg, C.P. *Goldblatt 436*
T. nelsonii Bak.	22	Linksfield Ridge, Johannesburg, Tvl. *Goldblatt 5.*
T. lineata (Salisb.) Ker	42	Alice, Eastern C.P. *Goldblatt 438*
T. flabellifolia (de la Roche) Lewis	22	McGregor, C.P. *Lewis 6203* (NBG)
Chasmanthe N.E. Br.		
C. aethiopica (L)N.E. Br.	32	(Nakajima, fide Darlington & Wylie 1955)
	20	Kirstenbosch, C.P. *Goldblatt 90* (J)
C. floribunda (Salisb.) N.E. Br.	20	ex hort. *Goldblatt 467*

All localities given are in South Africa unless otherwise stated. The provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are located at the Bolus Herbarium, Cape Town, unless stated to the contrary.

The taxonomic position of *Crocosmia paniculata*, previously regarded as a species of the genus *Curtonus*

Crocosmia paniculata, previously the only species in the monotypic genus *Curtonus*, is a tall, much branched plant with a bright orange, usually long-tubed zygomorphic flower. It occurs in the mountains of the eastern Transvaal and Natal. The diploid number of 22 and karyotype comprising small acrocentric chromosomes point to a relationship with species of *Crocosmia*, particularly *C. masonorum* and *C. mathewsiana* (fig. 27: G).

The similarity of the karyotype of *Curtonus* with its basic number of 11 to that of *Crocosmia* is not altogether rurprising, as *Curtonus* was regarded by Lewis (1954) as being intermediate between *Crocosmia* and the more specialised genus *Chasmanthe*. This similarity of karyotype must be regarded as confirmation of Lewis' suggestion on the affinity of *Curtonus*, although earlier workers separated it from *Crocosmia*.

Crocosmia paniculata was originally described as *Antholyza paniculata* by Klatt (1868) and was treated as such by Baker (1896). When *Antholyza* was revised by Brown (1932) he created the new genus *Curtonus* for this species. Hutchinson (1934) placed *Curtonus* in his tribe *Antholyzeae* which contained all the genera which Brown created out of *Antholyza*. The tribe *Antholyzeae* was thus as unnatural as the genus *Antholyza*. This classification left *Curtonus* and *Crocosmia* in different tribes until Lewis resolved the inconsistency.

Crocosmia paniculata is a fairly large plant regarded as unusual, as it has a stout stem with a slightly flexuose axis bearing many branches. The flower is also unusual for it has a somewhat curved perianth tube with a very narrow basal part and a hooded upper perianth segment.

A close examination of other species of *Crocosmia* reveals that all of these features occur in this genus: *C. aurea* and *C. mathewsiana* have a similar slightly flexuose stem with many branches; both *C. pottsii* and *C. mathewsiana* have a curved perianth tube; the upper segment in *C. mathewsiana* is slightly hooded. Thus it can be seen that *Curtonus* was a genus based on very inadequate grounds. The only unusual feature in *Curtonus* is the length of the perianth tube which is far longer than in any other species of *Crocosmia*. Thus it is proposed that *Curtonus paniculatus* should be regarded merely as a long-tubed species of *Crocosmia*. The necessary taxonomic corrections are made in a separate chapter.

TRITONIA

$2n = 22, 44.$

Tritonia is a large genus of about forty species which occurs throughout southern Africa. The plants are generally smaller in size than species of *Crocosmia*, are less branched and are distinguished from that genus by an elongated capsule containing many small seeds.

Nine species of *Tritonia* were examined and, as observed in *Crocosmia*, the karyotype is undistinguished. With the exception of *T. lineata*, all species have a diploid number of 22 (Table 15) and the chromosomes are fairly small ranging from 1,5 to 2,5μ. *T. lineata* has 44 chromosomes and must be regarded as a polyploid species. Several different populations of this species were examined and all have proved to be polyploid. The karyotypes of all the species are similar and the idiogram of *T. squalida* is represented here as characteristic of the genus (fig. 27: I—R). Although the chromosomes vary rather little in length, three pairs of longer chromosomes can be distinguished. Satellites are not always seen, but when visible, as in *T. squalida*, they are located on the longer chromosomes. A metacentric chromosome is not present but the karyotype bears unmistakable resemblance to that of *Crocosmia.*

Only one species of *Tritonia* has previously been studied. Brittingham (1934) found $2n = 20$ for *T. crocata* while Sharma & Sharma (1960) recorded $2n = 60$ and 22 in cultivated varieties of the same species. In the light of the present work where nine more species were studied, all having a basic number of 11, it seems that only the one record of Sharma & Sharma is correct. Brittingham may have overlooked a pair of chromosomes or he may have been dealing with some other plant.

One of the nine species studied here, *T. lineata*, proved to be polyploid. No meiotic examination was made, but the species is fertile and breeds true. This is one of the few polyploid species in the tribe *Ixieae* and again, as in *Ixia orientalis* the polyploid species of *Gladiolus*, it is significant to note that it occurs in the summer rainfall area.

CHASMANTHE

$2n = 20.$

Chasmanthe is a small genus occurring in the southern and western Cape Province. The plant is characterised by its very zygomorphic flower with a long perianth tube and a large, hooded upper perianth segment. Only two of the ten recognised species were studied. Both have a diploid number of 20 and the chromosomes are all comparatively small and acrocentric (fig. 27: S—T). In size the chromosomes range from 1,5 to 2,5μ and of these, four pairs appear somewhat larger in size. In both species a satellite was observed on one of the large chromosomes. The idiogram of *C. floribunda* is illustrated as representative of the genus (fig. 27: U).

Prior to this work there has been one cytological report in this genus. Nakajima (fide Darlington & Wylie 1955) reported $2n = 32$ for *C. aethiopica.* In the light of the present results of $2n = 20$ for *C. aethiopica* and *C. floribunda* it would appear that the plant studied by Nakajima belonged to another genus. It may have been a species of *Tritoniopsis* or *Anapalina* which have diploid numbers of 32 and 34, and which resemble *Chasmanthe* to some extent.

The two cytological reports for *Chasmanthe* in the present work can be regarded as new records and it is tentatively suggested that the basic number for the genus is 10.

The genus *Montbretiopsis*

Montbretiopsis florentiae, the only representative of this rare genus is a small plant in which the aerial part of the stem has been reduced and the flowers have a long perianth tube. Several attempts to collect this plant in the arid areas where it occurs were unsuccessful. Presumably the plant only flowers in seasons when the irregular rainfall has been sufficient. It was suggested by Lewis (1954) that the plant is allied to *Tritonia* and may even belong in this genus. It is hoped that a cytological examination will one day confirm or refute this view.

Possible phylogeny and evolution and the taxonomic affinity of *Chasmanthe*

It is clear from the similarity of the basic chromosome number and karyotype that *Tritonia* and *Crocosmia* are related. This is recognised by most authors, for these two genera are always placed next to one another in any treatment. The genera are so similar that there exists, even today, some confusion as to which species belong to which genus. N. E. Brown (1932) attempted to clarify the position by redefining both genera. Although several species have been described since, our knowledge is not yet complete enough to make it possible to decide whether *Crocosmia* is a valid genus or not. It seems that Brown's interpretation of the genera is essentially correct though it needs some modification. For the sake of convenience at least, the genus *Crocosmia* should be maintained.

The genus *Chasmanthe* was referred to *Petamenes* by Hutchinson (1934) and it was merged with *Anomalesia* and *Kentrosiphon* in *Petamenes* by Phillips (1941).

Chasmanthe does indeed resemble *Petamenes* in general floral structure for it has a similar long perianth tube with a slender basal and broad upper portion. The upper perianth segment is also very long and hooded as in *Petamenes*. The resemblance ceases here for the style and stigmas are different and the seeds are not winged as they are in *Petamenes*. The bracts resemble those of Tritonia while the large capsule containing few seeds and the corms are like those of *Crocosmia* and perhaps *Curtonus*.

Lewis (1954) regarded *Chasmanthe* as being most closely allied to *Crocosmia* and *Curtonus*. She considered *Chasmanthe* as the most specialised and advanced of the evolutionary line beginning with *Tritonia* and *Crocosmia*. The karyological evidence supports her interpretation more strongly than any other, for although the karyotype resembles that of *Tritonia* and *Crocosmia* in general size and appearance of the chromosomes, the basic number is 10, compared to 11 in *Tritonia* and *Crocosmia*. If Lewis' interpretation is correct, *Chasmanthe* has probably evolved from a *Crocosmia*-like ancestor, possibly *C. paniculata* by modification of the floral parts. During this process aneuploid reduction could also have occurred to produce the karyotype of *Chasmanthe*.

Cytological examination has confirmed the close relationship of *Tritonia* and *Crocosmia* (and *Curtonus*) and suggests the possible relationship of *Chasmanthe*.

It is suggested that these genera, together with *Montbretiopsis*, all of which seem to belong to a single phylogenetic line, be grouped in a new subtribe called *Tritonineae*. Previously these genera were placed in the *Ixiineae* of Lewis (1954) but as has been shown, cytological results reveal the presence of several lines within her subtribe (note the section on *Dierama* and allies).

Evolution in this group parallels that in *Dierama*. Species of *Crocosmia*, which are large plants occurring in the eastern mountains of southern Africa, appear to have given rise to *Tritonia* which is generally much smaller and occurs mainly in the winter rainfall area. Species of *Tritonia* appear to be more specialised and to grow in more arid conditions. *Chasmanthe* seems to be the most modified of all and it occurs in the winter rainfall area in the western Cape Province.

h. Subtribe ***Babianineae***

Babiana and *Antholyza* (including *Anaclanthe*)

This group comprises fairly small plants which have a very characteristic appearance: the leaves are pleated; the corms deep seated and covered by particularly tough tunics; pubescence occurs on all or some of the aerial organs.

BABIANA

$2n = 14.$

This is a large genus comprising about sixty species. It is found mainly in the winter rainfall area of the Cape Province, but representatives occur in the summer rainfall area of southern Africa and on the island of Socotra. The genus is fairly variable, both actinomorphic and zygomorphic species occur, though the degree of zygomorphy is less pronounced than in the other genera in this group.

Eleven species were examined by the present author and were found to have a diploid number of 14. Two exceptions were found, namely *B. sambucina* and *B. hypogea*, where supernumerary chromosomes were sometimes found in populations of these species. These will be discussed below.

The karyotypes of all the species of *Babiana* examined are similar (fig. 28: A—J). The centromeres are all sub-terminal, thus the chromosomes can be described as acrocentric, and the range in size is from 1,5 to just less than 5μ. There are two pairs of long chromosomes, the one pair being about 4,5μ long and the shorter measuring 3,5 to 4μ. This shorter one possesses a satellite. The remaining five pairs range from under 3 to 1,5μ, and the second in length of

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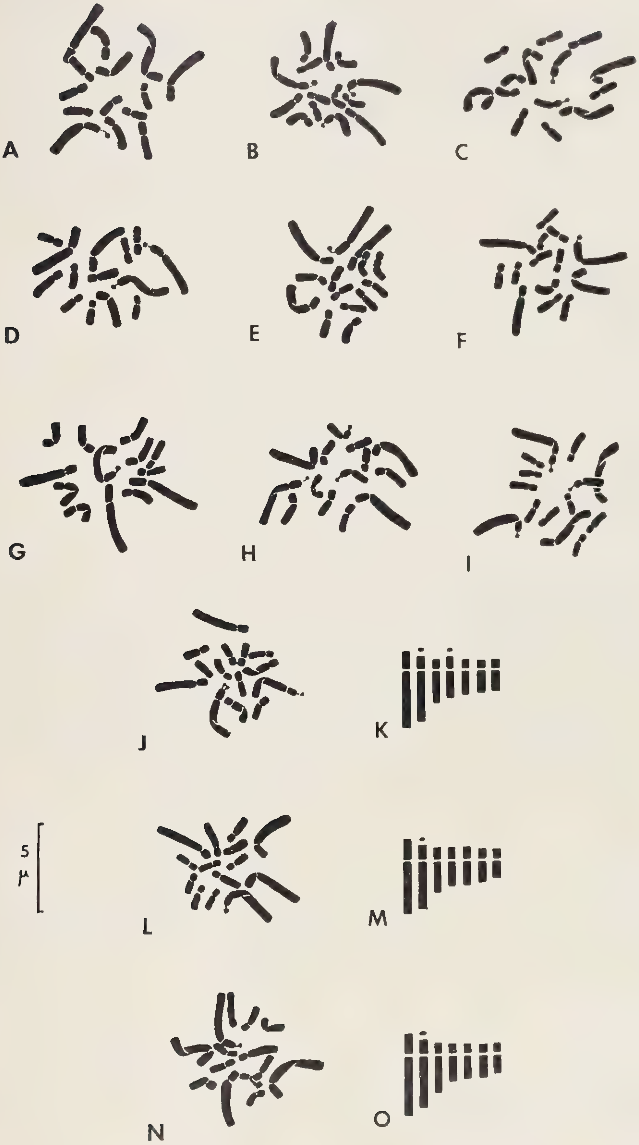
FIG. 28.

Karyotypes of *Babiana* and *Antholyza* (including *Anaclanthe*). A. *Babiana villosula;* B. *B. nana;* C. *B. scabrifolia;* D. *B. flabellifolia;* E. *B. vanzyliae;* F. *B. pubescens;* G. *B. sambucina;* H. *B. stricta;* I. *B. tubulosa;* J. *B. mucronuta;* K. Idiogram of *Babiana;* L. *Antholyza plicata* = *Anaclanthe*); M. Idiogram of *A. plicata;* N. *Antholyza ringens;* O. Idiogram of *A. ringens.*


A
B
C
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H
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K
5 μ
L
M
N
O

Table 16

Chromosome numbers in *Babiana* and *Antholyza.*

Species	Diploid No.	Collection Data or Reference
Babiana Ker		
B. disticha Ker	14	(Fernandes & Neves 1961)
B. flabellifolia Harv. ex Klatt	14	Calvinia, C.P. *Goldblatt 244*
B. hypogea Burch.	14+1–3B	Johannesburg, Tvl. *Goldblatt 16* (J)
	14	Witbank, Tvl. *Makunga* (Fort Hare)
	14 + B	Blyde Canyon, Tvl. *Davidson sn.* (J)
(as B. bainesii)	14	(Riley 1962)
B. mucronata (Jacq.) Ker	14	Citrusdal, C.P. *Goldblatt 248*
B. nana (Andr.) Spreng.	14	Darling, C.P. *Goldblatt 197*
B. pubescens (Lam) Lewis	14	Namaqualand, C.P. *Goldblatt 18* (J)
B. pulchra (Salisb.) Lewis (as B. atrocyanea)	14	(Zucconi 1956)
B. purpurea (Jacq.) Ker	14	(Zucconi 1956)
B. pygmaea (Burm. f.) N.E. Br. (as B. macrantha)	14	(Zucconi 1956)
B. rubrocyanea (Jacq.) Ker (as B. stricta v. rubrocyanea)	14	(Zucconi 1956)
B. sambucina (Jacq.) Ker	14 (+1–2B)	Clanwilliam, C.P. *Goldblatt 19* (J)
	14	(Zucconi 1956)
B. scabrifolia Brehm ex. Klatt	14	(ex hort) *Goldblatt 97* (J)
B. stricta (Art) Ker	14	Llandudno, C.P. *Goldblatt 43* (J)
	12	(Brittingham 1934)
	14	(Sugiura, fide Darlington & Wylie 1955)
	14+B	(Zucconi 1956)
B. stricta var. erectifolia Lewis (as B. erectifolia)	14	(Gwynn 1958)
B. stricta var. sulphurea (Jacq.) Bak. (as B. sulphurea)	14	(Sharma & Sharma 1960)
B. tubulosa (Burm. f.) Ker		Springbok, C.P. (ex hort) *Goldblatt 512*
B. tubulosa var. tubiflora (L.f.) Lewis (as B. tubiflora)	14	(Zucconi 1956)
	14	(Gwynn 1958)
B. vanzyliae L. Bol.	14	Nieuwoudtville, C.P. *Goldblatt 103* (J)
B. villosula (Gmel) Ker ex Steud		Oudekraal, C.P. *Goldblatt 89* (J)
B. villosa (Ait.) Ker	14	Oudekraal, C.P.
B. atrocyanea (an unknown species)	14	Zucconi (1956)
Antholyza L.		
A. ringens L.	14	Fish Hoek, C.P. *Goldblatt 83* (J)
A. plicata L.f.	14	Lamberts Bay, C.P. *Goldblatt 113* (J)

All localities are in South Africa and the provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are located at the Bolus Herbarium, Cape Town, unless stated to the contrary.

these 5 pairs can sometimes be seen to bear a satellite. This character was noted in only four of the eleven species examined and thus does not seem to be a constant feature. However, it was probably overlooked in the other species, as satellites are not always clearly visible and often only one of a pair of satellities is seen.

As the karyotypes of the species vary only very little, a generic karyotype can be constructed. Here the idiogram of the karyotype of *B. stricta* is shown as representative of the genus (fig. 28: K). Other species do differ but the variation is minimal. Small size differences occur and there are slight changes in the position of the centromere and, as mentioned, the second satellite is not always seen. The variation is not significant for this study though it may be useful in a critical evaluation of *Babiana* alone.

The supernumerary of B chromosomes in *Babiana*

The variation in chromosome number in *B. sambucina* and *B. hypogea* follows a pattern found in several groups of plants. The extra chromosomes vary in number; even in the same root tip one, two or none can be found (fig. 29). This is typical of the behaviour of the so called B chromosomes. The reason is that these chromosomes frequently lag behind at anaphase.

Three populations of *B. hypogea* were examined. One from Witbank, Transvaal, had no B chromosomes. Populations from the eastern Transvaal escarpment, near Blyde River Canyon, had one or no extra chromosomes, while a population from Melville, Johannesburg, had one, two, three and sometimes even four. The significance of the B chromosomes is unknown and their occurrence does not seem to be correlated with morphological differences or climatic conditions.

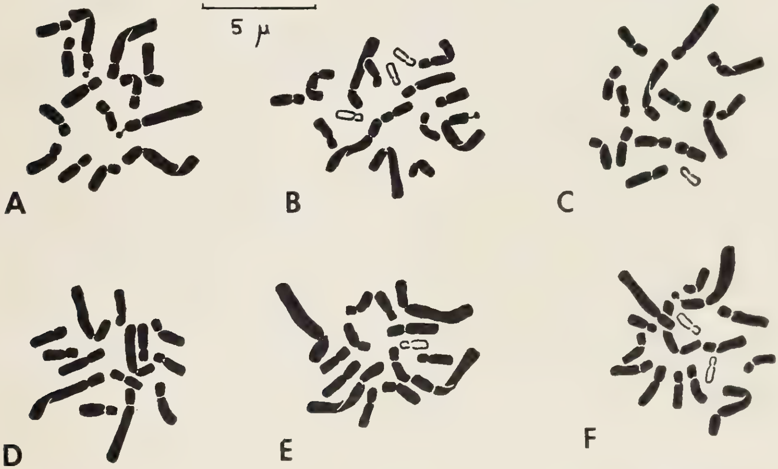

Fig. 29.

B chromosomes in *Babiana*. A – C metaphase plates of plants from a single population of *B. sambucina* showing none to three B chromosomes; D – F metaphase plates of plants from three different populations of *B. hypogea*, from Witbank, Transvaal; Blyde Canyon, Transvaal, and Johannesburg respectively.

The cytology of *Babiana* has been studied quite extensively. It is clear from the existing work that the diploid number is 14 for all species so far examined (Table 16). Of the eleven species studied by the present author, seven of the chromosome counts are new records and the remaining four, for *B. stricta*, *B. tubulosa*, *B. sambucina* and *B. hypogea* confirm the earlier reports. The occurrence of B chromosomes in *Babiana* was first recorded by Zucconi for *B. stricta*. These supernumerary chromosomes were again found by the present author in some populations of *B. hypogea* and *B. sambucina*. Although their significance is not known they play no part in phylogenetic considerations and thus are unimportant in the present study.

Thus, the total of seventeen species (plus one of unknown identity, *B. atrocyanea*) has been examined. Where the studies of earlier workers were sufficiently detailed, it can be seen that the karyotype for the genus as described in this work, confirms their results. The only conflicting report is that of Brittingham (1934) who found a diploid number of 12 in *B. stricta*. Since this species has been found by other workers to have a diploid number of 14, it seems that Brittingham's count was erroneous. A close examination of his illustration shows a pair of very long chromosomes with a median constriction. As this type of chromosome has not otherwise been recorded in *Babiana*, it is likely that this in fact represents two short chromosomes lying close together.

Babiana consists of sixty species thus it can be seen that a fair proportion of the genus has been studied. As there is no variation (apart from the report of Brittingham) it seems that a basic number of 7 for the genus can confidently be proposed.

ANTHOLYZA (including *Anaclanthe*)

$2n = 14.$

Antholyza, as treated here, is a small genus of two or perhaps three species occurring only in the western Cape Province. The flowers are modified, having a long upper segment sheathing the stamens and style, and reduced lower segments. The diploid number is 14 and as in *Babiana* the karyotype consists of 2 pairs of long chromosomes and 5 pairs of shorter ones. Satellites were observed on the second longest pair only. The karyotypes of *A. ringens* and *A. plicata* (previously *Anaclanthe*) are very similar and fit within the pattern observed for *Babiana*. The karyotype of this genus is described here for the first time. As can be seen from fig. 28, the karyotypes are very similar to those of *Babiana*.

Discussion

The morphological similarities between *Babiana*, *Anaclanthe* and *Antholyza* are striking; all have plicate leaves, a feature not common in the Iridaceae; some degree of pubescence, particularly on the stem and bracts, is present; the corm is unique in the family, having peculiar tough papery tunics which extend upwards in a neck around the base of the stem; and the firm green bracts have brown tips. The difference between the genera is in the structure of the flower which is increasingly specialised and zygomorphic in *Anaclanthe* and *Antholyza* (fig. 30). In *Babiana* the flower structure ranges from actinomorphic to slightly zygomorphic. Species with the latter type of flower have a straight perianth tube slightly expanded at the throat. The posterior or upper perianth segment is somewhat larger than the others and widely separated from them, forming a slight hood. The upper lateral segments are partly united with the three lower segments, the latter forming a lip (fig. 30: A, B).

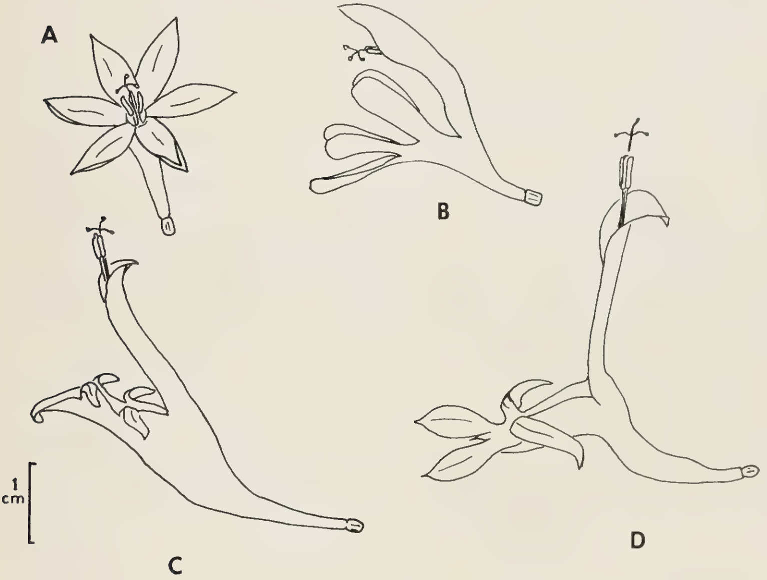

FIG. 30.
Flower structure in *Babiana* and its allies. A. *Babiana stricta;* B. *B. fimbriata;* C. *Antholyza plicata* (*Anaclanthe*)*;* D. *Antholyza ringens.*

This type of flower is rather different from that found in *Antholyza* and is extremely modified (fig. 30: C, D). The perianth tube is long and bent upwards. The hood-like posterior segment is much larger than the other segments and envelops the lower part of the stamens and style. The other segments are partly united with the three lower ones forming a lip. The same type of flower occurs both in *A. plicata* and *A. ringens*, but in the latter the zygomorphic trend is accentuated (fig. 30: D). The upper segment is larger than in *A. plicata* and is more widely separated from the other segments which are united for most of their length. The upper lateral segments are reflexed while the lower lateral segments form a large lip and the lower segment is much reduced. In *A. ringens* the inflorescence is also modified in that the main stalk is sterile and stands erect bearing a few bracts only, while a lower branch bears the flowers.

Thus, while the distinct flowers of *Anaclanthe* and *Antholyza* have served as the basis for the recognition of these two genera, they have tended to disguise their correct relationships. The difficulty is paralleled in the relationship between *Gladiolus* and *Crocosmia* and their respective more zygomorphic allies. The problem has been resolved in the same way by reducing the number of genera with zygomorphic flowers. These genera are often very small but should be maintained as distinct from the presumed parent genus both for convenience and in recognition of their very specialised flower. Accordingly, *Anaclanthe* has been included in *Antholyza* by the present author.

Taxonomic History

The genus *Antholyza* has had a very confused taxonomic history. The relationship between the type species, *A. ringens* and *Babiana* has often been misunderstood and these two obviously allied genera have at times been placed in different tribes. The second species of *Antholyza* studied here, *A. plicata*, has been transferred by the present author from *Anaclanthe* back to *Antholyza*. This species was in fact referred to *Antholyza* when first described by the younger Linnaeus, but was subsequently treated as a *Babiana* by most authors.

Diels (1930) recognised the similarities between *Babiana*, *Antholyza* and species previously referred to as *Anaclanthe*. He placed the species of the latter two genera in a separate section of *Babiana*. Diels upheld the genus *Antholyza* although without the type species *A. ringens* this was taxonomically invalid. When Brown (1932) revised the genus *Antholyza* (sensu Baker), he ignored Diel's view. Instead he recognised *Antholyza ringens* as the only species in this genus and created the new genus *Anaclanthe* for *A. ringens*. Hutchinson (1934) followed Brown's treatment and placed *Anaclanthe* and *Antholyza* in the tribe *Antholyzeae* with the other members of Baker's *Antholyza*, while referring *Babiana* to a separate tribe. Lewis (1954) recognised the true affinities of the three genera and placed them in her subtribe *Babianineae*. Her treatment, which takes into account all morphological features, results in a more natural classification which is confirmed by cytological evidence.

As *Antholyza* and *Anaclanthe* are morphologically so similar to *Babiana* and share a common karyotype unique in the family, Lewis' subtribe *Babianineae* has been maintained. *Anaclanthe* has now been incorporated in *Antholyza* so that this subtribe comprises only two genera, *Babiana* and *Antholyza*, the latter distinguished from Babiana by its very specialised flowers.

i. Subtribe ***Exohebeineae***

Tritoniopsis and *Anapalina*

This subtribe consists of a pair of closely related genera, occurring in the mountains of the winter rainfall area of the Cape Province. The plants are typically summer flowering, when the spicate inflorescences of colourful flowers are often conspicuous. *Tritoniopsis* is the less modified, having actinomorphic to slightly zygomorphic flowers with a short perianth tube, while *Anapalina* has a long tube and a large hooded upper perianth segment.

TABLE 17

Chromosome numbers in *Tritoniopsis* and *Anapalina.*

Species	Diploid No.	Collection Data or Reference
TRITONIOPSIS L. Bol		
T. leslei L. Bol.	32	Cascades, Ceres, C.P. *Goldblatt 409*
T. lata (L. Bol.) Lewis	32	Betty's Bay, C.P. *Goldblatt 186*
T. parviflora (Jacq.) Lewis	32	Silvermine Plateau, C.P. *Goldblatt 410*
T. unguicularis (Lam.) Lewis	32	Silvermine Plateau, C.P. *Goldblatt 411*
ANAPALINA N.E. Br.		
A. nervosa (Thunb.) Lewis	34	Nieuwoudtville, C.P. *Goldblatt 286*
A. triticea (Burm. f.) N.E. Br.	34	Constantia Nek, C.P. *Goldblatt 403.*

All specimens were collected in the Cape Province, South Africa, and are housed at the Bolus Herbarium, Cape Town.

TRITONIOPSIS

2n = 32.

The genus *Tritoniopsis* comprises fourteen species. Four species were examined in this study and all were found to have a diploid number of 32 (Table 17). As can be seen from fig. 31 : A—D, the karyotypes have no remarkable features. All the chromosomes are acrocentric and uniformly small, ranging from 1 to 1,5μ in length.

ANAPALINA

2n = 34.

Two of the seven species in this small genus were studied (Table 17). In both the diploid number was found to be 34. The karyotypes comprise small acrocentric chromosomes ranging in length from 1 to 1,5μ (fig. 31 : E, F).

The affinities of *Tritoniopsis* and *Anapalina*

These two genera are closely allied and form a natural group. They are unique in the Iridaceae in posessing the following series of characteristics: coriaceous leaves bearing several distinct main veins; dry, firm bracts and bracteoles of which the latter are longer, inflated capsules bearing light seeds with

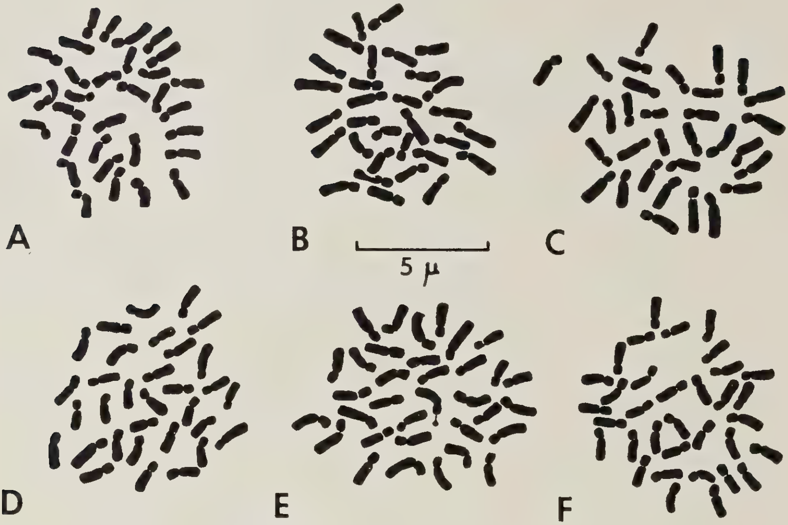

Fig. 31.

Karyotypes of *Tritoniopsis* and *Anapalina*. A. *Tritoniopsis* leslei; B. *T. lata;* C. *T. parviflora;* D. *T. unguicularis;* E. *Anapalina nervosa;* F. *A. triticea.*

a spongy testa and a wing. All the species in the two genera are summer flowering whether they occur in the summer or winter rainfall areas. This is unusual in the *Iridaceae*, especially as the great majority of species occur in the winter rainfall region.

Lewis (1954) suggested that *Tritoniopsis* and *Anapalina* were members of a single phylogenetic line in which *Tritoniopsis* was the more primitive. This seems reasonable, for as she points out, *Tritoniopsis* appears to be less specialised both in the flower and the inflorescence. Branching of the peduncle is common in *Tritoniopsis* but does not occur in *Anapalina*. The flower is either regular or slightly zygomorphic with a short perianth tube in *Tritoniopsis*. In contrast the flower in *Anapalina* is extremely zygomorphic with perianth parts of different lengths, a long curved perianth tube which has an unusual narrow basal portion and an expanded upper portion. This feature of the perianth tube is paralleled in *Homoglossum*, *Petamenes*, *Anaclanthe* and *Antholyza*, and this prompted Hutchinson (1934) to place these genera in a separate tribe apart from the less specialised genera which they otherwise resemble.

Tritoniopsis and *Anapalina* have a series of characteristics which make them appear a quite distinct group of the *Ixieae*. There do not seem to be any morphological similarities with other genera that point to a phylogenetic relationship, nor do cytological features help in this respect. The cytological data confirm that these two genera belong within the tribe *Ixieae* on general size of chromosomes. The diploid numbers of 32 and 34 encountered in these genera are the highest found in the tribe and the karyotypes are perhaps most similar to *Gladiolus* and its allies ($2n = 30$). However, morphological evidence will not support any suggestion of a relationship here.

Anapalina and *Tritoniopsis* are clearly a pair of closely related genera sharing many unique morphological features and having distinct yet similar karyotypes. As suggested by Lewis (1954) these genera form a distinct subtribe which she called *Exohebineae*, a name based on *Exohebea*, a genus now incorporated in *Tritoniopsis*. It seems plausible in the light of Lewis' suggestions on the evolution of the group, that *Anapalina* evolved from an ancestor rather like *Tritoniopsis* in a process which involved the increase in chromosome number, i.e. increasing aneuploidy. In the light of this suggestion it would be interesting to try to breed intergeneric hybrids and observe their meiotic behaviour. This will prove a difficult undertaking as both *Tritoniopsis* and *Anapalina* are notoriously difficult to cultivate and their natural habitat is often rather isolated as they usually grow at high altitudes.

5. SUMMARY OF TAXONOMIC PROPOSALS

a. CLASSIFICATION OF THE FAMILY INTO TRIBES AND SUBTRIBES

It is suggested that the division of the family into three tribes be followed. The tribes proposed by Bentham & Hooker are supported except for the exclusion of one subtribe (*Croceae*) from their second tribe. Their definition of the tribes on the nature of the inflorescence and secondarily, on the position of the stamens relative to the style branches can be correlated with marked differences in chromosome size in these groups. The proposed system is illustrated diagrammatically in figures 32 and 33.

Tribe 1. **Sisyrinchieae** Bentham & Hooker.

Stamens alternate to stigma lobes; style unbranched or branched; branches entire; inflorescence consisting of cymes enclosed in large bracts, and variously grouped together; rootstock unmodified or a rhizome. Chromosomes small or medium in size.

The southern African genera can be treated as comprising two subtribes distinguished on both morphological and cytological grounds. Neither Weimarck nor Lewis can be followed in their placing of the woody genera in a separate tribe, as the cytology reveals that they are allied to *Aristea*.

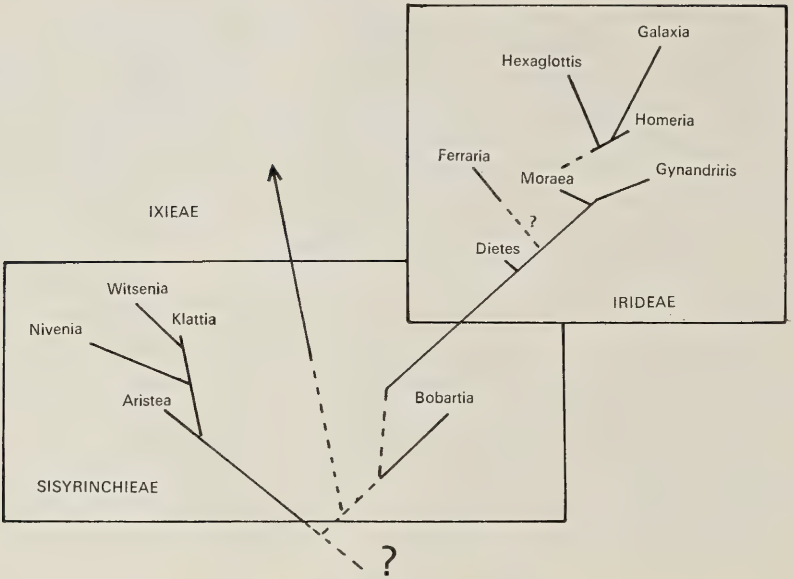

FIG. 32.

Diagram showing suggested phylogenetic inter-relationships of the tribes of the Iridaceae. The relationship of the South African representatives of the Irideae and Sisyrinchieae is also shown.

Subtribe 1. **Aristeineae** Bentham & Hooker (as *Aristeae*)

Style undivided or shortly branched; flowers fugaceous or long lived; rootstock a creeping rhizome or an erect woody stem. Chromosomes small, basic number 16.

Genera recognised: Aristea, Nivenia, Witsenia, Klattia. The latter three genera are woody and exhibit secondary growth. This subtribe may also include several Australian genera such as *Patersonia* (n = 12).

Subtribe 2. **Sisyrinchiineae**

Style branched; flowers fugaceous; rootstock a creeping rhizome. Chromosomes small to medium sized, basic chromosome number 10 in *Bobartia.*

Genera recognised: Only one South African representative, *Bobartia.* This genus is included in this tribe of predominantly New World elements but it may later be found that it should be referred to a separate monotypic subtribe of its own.

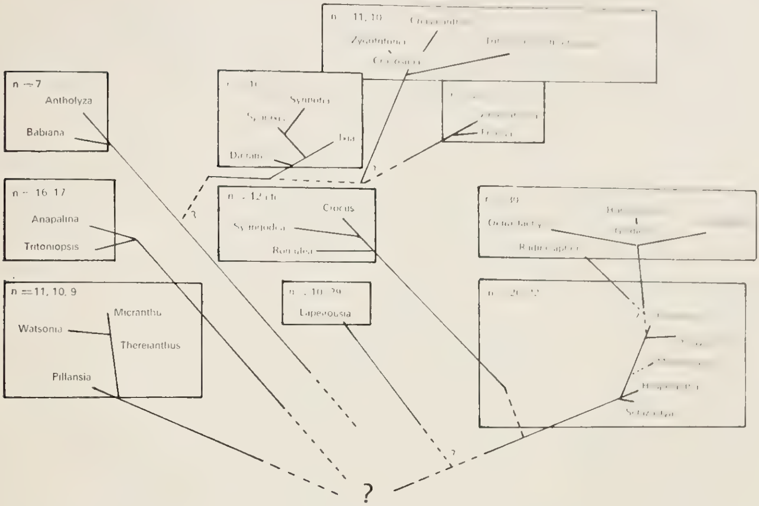

FIG. 33.

Diagrammatic representation of the phylogeny and inter-relationships of the genera of the tribe Ixieae. Each subtribe is contained within a block.

Tribe 2. **Irideae**

Stamens opposite style branches; style usually branched and branches divided; inflorescence consisting of cymes enclosed in large bracts, and grouped together variously, flowers occasionally solitary; rootstock a rhizome, bulb or single internode corm. Chromosomes characteristically large.

This tribe (the *Moraeeae* of Bentham & Hooker) comprises both African, European and New World elements. The African genera are suggested as comprising three subtribes.

Subtribe 1. **Iridineae**

Style three-branched, petaloid, branches terminating in two crests; perianth segments unguiculate, and inner usually erect and smaller than outer; limb of outer segments reflexed; rootstock a rhizome, bulb or corm; stamens free or filaments connate. Chromosomes large, basic number 10 but many other numbers occur.

Genera recognised: Dietes, Moraea, Gynandriris in Africa and *Iris* and its close allies in the northern hemisphere. Suggestions that *Dietes* be placed in *Moraea* and that *Gynandriris* be transferred to Iris are shown on cytological and morphological grounds to be incorrect.

Subtribe 2. **Homeriineae** Goldblatt subtribes nov.

Stylus subpetaloideus, ramosus et befidus vel non petaloideus et simplex aut profunde divisus; perianthii segmenta subaequales, segmenta non unguiculata interiora non erecta; caudex cormus; filamenta connata. Chromosomata magna, numeri basici 6 et 8.

Type genus: *Homeria* Vent.

Style subpetaloid branched and forked or not petaloid and simple or deeply divided; perianth segments not unguiculates, subequal, inner segments not erect; rootstock a tunicate corm; filaments connate. Chromosomes large, basic numbers 6 and 8.

Genera recognised: Homeria, Hexaglottis, Galaxia.

Subtribe 3. **Ferrariineae** Goldblatt subtribus nov.

Stylus petaloideus, tribus ramis, apice plumoso; perianthii segmenta subaequales, segmenta reflexa; caudex cormus persistens, munitus tunicis tenuioribus; filamenta connata. Chromosomata magna, numerus basicus 10.

Type genus: *Ferraria* L.

Style petaloid, three branched with a dissected feathery apex; perianth segments subequal, reflexed; rootstock a corm; filaments connate. Chromosomes large, basic number 10.

Genera recognised: Ferraria.

This may be allied to several New World genera such as *Tigridia* but further investigation is needed. Differences in cytology and morphology are such that they do not in the author's opinion, support any contention that *Tigridia* is closely related to *Ferraria.*

Tribe 3. **Ixieae** Bentham & Hooker

Style always branched; inflorescence usually a spike (of solitary cymes), sometimes reduced to a single flower; rootstock usually a several internode corm (a rhizome in one genus). Chromosomes characteristically small.

Mainly an African group with only three genera known to extend into Europe and Asia. The subtribes are recognised on cytological grounds but also on correlated morphological features which often are very characteristic.

The subtribes are sometimes difficult to define morphologically when there are only rather minor features to distinguish them.

Subtribe 1. **Watsoniineae** Lewis ex Goldblatt subtribus nov.

Rami styli fucati; cormus rotundus vel aplanatus munitus tunicis reticulatis fibris tenacis; folia equitantia, usitate tenaces et fibrosa. Numeri basici chromosomatum 11, 10, 9.

Type genus: *Watsonia* Miller.

Characterised by bifid style branches; corms rotund to flattened with reticulate tunics of coarse, tough fibres; leaves equitant, usually tough and fibrous; flowers usually arranged distichously. Basic chromosome numbers 11, 10, 9.

A decreasing aneuploid series is suggested in the group where each genus with a lower basic number has a more modified structure.

Genera recognised: Pillansia, Thereianthus, Micranthus, Watsonia. The proposed subtribe *Pillansiineae* of Lewis is not recognised, but is included here.

Subtribe 2. **Lapeirousiineae** Goldblatt subtribus nov.

Rami styli furcati; cormus campanulatus base plana, munitus tunicis duris lignosis, paginis asperis atque base plana integra; folius basalis solum unus, lanceolatus costatus. Numeris basici chromosomatum 10, 9?

Type genus: *Lapeirousia* Pour.

Style branches bifid; corms campanulate, flat based with tunics of hard woody material with a rough surface, also flat based and entire; basal leaf one only, lanceolate and ribbed. Basic chromosome numbers 10, 9?

Genera recognised: Lapeirousia sensu stricto (not including *Anomatheca*).

The subgenus *Anomatheca* included by Baker in *Lapeirousia* has been reinstated as a genus. Its affinities are with *Freesia* rather than with *Lapeirousia*, as evidenced by morphological and cytological data. *L. fistulosa* previously referred to the subgenus *Ovieda* of *Lapeirousia* was shown to be a member of *Anomatheca*, and has been transferred to this genus.

Subtribe 3. **Hesperanthineae** Goldblatt subtribus nov.

Rami styli integri vel longiores stylis vel breviores; caudex rhizome brevis vel cormus campanulatus base plana, asymmeticus radicibus emergentibus crestis lateralis exceptus *Melasphaerula*, tunicis duris integris lignosis paginis laevis; folia equitantis ad teretia vel cruciformia, pauces ad plures. Numerus basicus chromosomatum 13 sed 11 in *Melasphaerula*.

Type genus: *Hesperantha* Ker.

Style branches entire and either longer or shorter than the style; rootstock a short rhizome or a campanulate, flat based and asymmetric corm with the roots emerging from a lateral crest except in *Melasphaerula*, tunics hard, woody and entire with a smooth surface; leaves equitant to terete or cruciform, few to many. Basic chromosome number 13, to 11 in *Melasphaerula*.

Genera recognised: Schizostylis, Hesperantha, Geissorhiza, Engysiphon and *Melasphaerula*.

Subtribe 4. **Crocineae** Bentham & Hooker (as *Croceae*)

Style branches various, unbranched, bifid or multifid; corms asymmetric to symmetric, variously shaped, tunics entire, woody, sometimes papery or fibrous in *Crocus;* leaves slender and modified, either four channelled or terete or bifacial. Inflorescence reduced and flowers solitary on branches or inflorescence unbranched and aerial peduncle lacking; somatic chromosome number varied, and aneuploidy very common. Chromosomes small but often very large in Crocus. Suggested original basic number 12.

Genera recognised: Romulea, Syringodea, Crocus. The latter genus has been included here although this genus is the exception in the tribe, some species having very large chromosomes.

Subtribe 5. **Gladiolineae** Goldblatt subtribus nov.

Rami styli integri usitate expansi in lamella bilobata; cormus rotundus munitus tunicis vel duris marginibus basalis serratis vel papyraceis integrisque; folia vel plures et ensiformia vel unus, gracilis et linearis; bractea usitate magna, herbacea; semina usitate alata. Numerus basicus chromosomatum 15.

Type genus: *Gladiolus* L.

Style branches entire, usually expanded into a bilobed lamella; corm spherical, tunics either hard and split at the basal margins or papery and entire; basal leaves either many and ensiform or single, slender and linear; bracts herbaceous; flowers usually secund, seeds usually winged. Basic chromosome number 15.

Genera recognised: Gladiolus, Homoglossum, Oenostachys, Anomalesia and *Radinosiphon.*

There have been several treatments of the group of genera allied to *Gladiolus.* The genera recognised here are all closely related to *Gladiolus*, and given generic rank for the sake of convenience. Some reduction in the number of genera has been made and the following are changed in circumscription.

(i) *Homoglossum* is maintained, including *Petamenes abbreviatus*, the type species for the latter genus.

Homoglossum can be distinguished as follows: perianth tube long, basal portion slender widening abruptly to a tubular upper portion with a sac at the junction; leaves only one, slender, usually cruciform in section: corms small and having rather woody serrated outer tunics.

(ii) *Oenostachys* is enlarged to include the remaining species of *Petamenes* except *P. buckerveldii* which it is proposed be transferred to *Gladiolus.*

(iii) *Anomalesia* is also enlarged to include the monotypic genus *Kentrosiphon.*

(iv) *Gladiolus* itself is expanded to include the tropical African genus *Acidanthera.*

Subtribe 6. **Ixiineae**

Style branches entire with variously expanded apices; corm spherical with tunics of reticulate fibres of various thickness; leaves several, ensiform; bracts membranous, often dry and lacerated; seeds round and often shiny. Basic chromosome number 10.

Genera recognised: Dierama, Ixia, Sparaxis and *Synnotia.*

The last genus is maintained tentatively on rather doubtful grounds of convenience.

Subtribe 7. **Freesiineae** Goldblatt subtribus nov.

Rami styli furcati; cormus rotundus vel conicus munitus tunicis reticulatis fibris tenuibus; folia duo ad plures, equitantes, ensiformia, molles; capsula usitate pagina aspera; semina rotunda, nitida. Numerus basicus chromosomatum 11.

Type genus: *Freesia* Klatt

Style branches forked; corm spherical to conic with tunics of fine reticulate fibres; leaves two to many, equitant, ensiform, soft in texture; capsule usually with a rough surface bearing round shiny seeds. Basic chromosome number 11.

Genera recognised: Freesia, Anomatheca (previously regarded as a subgenus of *Lapeirousia*).

Subtribe 8. **Tritoniineae** Goldblatt, subtribus nov.

Rami styli integri vel apices bifidi; cormus rotundus ad aplanatus munitus tunicis fibris reticulatis; folia plures, equitantia, usitate molles. Numerus basicus chromosomatum 11 sed 10 in *Chasmanthe.*

Type genus: *Tritonia* Ker.

Style branches entire or slightly divided at the apex; corm round to flattened with tunics of reticulate fibres; leaves several, equitant and usually soft in texture. Basic number 11 but 10 in *Chasmanthe.*

The genus *Curtonus* has been incorporated in *Crocosmia* on grounds of morphological as well as cytological similarity. Two genera, *Montbretiopsis* and *Zygotritonia* which were not examined cytologically by the present author are believed to be allied to *Tritonia* and are included in this subtribe. Further examination may reveal that the monotypic *Montbretiopsis* should be included in *Tritonia.*

Genera recognised: Tritonia, Crocosmia (including *Curtonus*), *Chasmanthe, Zygotritonia* and *Montbretiopsis.*

Subtribe 9. **Babianineae** Lewis ex Goldblatt, subtribus nov.

Rami styli integri; cormus rotundus munitus tunicis subintegris, tenacis; folia ensiformia, plicata, usitate pubescentes. Numerus basicus chromosomatum 7.

Type genus: *Babiana* Ker.

Style branches entire; corm spherical with papery, tough almost entire tunics; leaves ensiform but almost always pleated and pubescent. Basic chromosome number 7.

Genera recognised: Babiana, Antholyza (including *Anaclanthe*).

The genus *Anaclanthe* is incorporated in *Antholyza*, for although it resembles *Babiana* as well, its extreme zygomorphy indicates that it is best included in *Antholyza*.

Subtribe 10. **Exohebineae** Lewis ex Goldblatt, subtribus nov.

Rami styli usitate integri, graceles; cormus magnus, rotundus munitus tunicis reticulatis fibris; folia prominentibus nervis, usitate lanceolata basi gracile, petioloidea; bractea externa proprie brevior quam interna; semina saepe inflata. Numeri basici chromosomatum 16, 17.

Type genus: *Tritoniopsis* L. Bolus.

Style branches usually entire and slender; corms large, spherical with very matted tunics of coarse fibres; leaves usually lanceolate with a slender petiole-like base, bearing several prominent veins; outer bracts characteristically shorter than the inner; seeds often with an inflated testa. Basic numbers 16, 17.

Genera recognised: Tritoniopsis (including *Exohebea*) *Anapalina.*

b. NEW NAMES PROPOSED AS A RESULT OF THE PRESENT STUDY

1. The subgenus *Anomatheca* is recognised here as a valid genus. The following taxonomic changes are necessary:

Anomatheca verrucosa (Vog. in Trew) Goldblatt comb. nov.
Ixia verrucosa Vog. in Trew, Pl. Rar. t 24 (1784), basionym.
Anomatheca juncea (L.f.) Ker in K. & S. Ann. Bot. 1: 227 (1805).
Lapeirousia juncea (L.f.) Ker in Bot. Mag. t 606 (1803).
Gladiolus junceus L.f. Suppl.: 99 (1781) non Burm.f. (1768).

The basionym of *Anomatheca juncea*, namely *Gladiolus junceus* L.f. is a later homonym of *G. junceus* Burm.f. Accordingly the epithet is illegitimate. The next available synonym is *Ixia verrucosa* Vogel in Trew, which is now taken as the basionym for the new combination.

Anomatheca laxa (Thunb.) Goldblatt comb. nov.
Gladiolus laxus Thunb. Flora Cap.: 15 (1823), basionym
Lapeirousia laxa (Thunb.) N.E.Br. in J. Linn. Soc. Bot. 48: 20 (1928)

Anomatheca fistulosa (Spreng. ex Klatt) Goldblatt comb. nov.

Ovieda fistulosa Spreng, ex Klatt in Linnaea 32: 781 (1863) basionym.
Lapeirousia fistulosa (Spreng, ex Klatt) Bak. in J. Linn. Soc. Bot. 16: 155 (1877)

Anomatheca grandiflora Bak. in Journ. Bot. 5: 337 (1876)
Lapeirousia grandiflora (Bak.) Bak. in Bot. Mag.: t. 6924 (1887)

Anomatheca viridis (Ait.) Goldblatt comb. nov.
Gladiolus viridis Ait., Hort. Kew. ed. 1, 3: 481 (1789), basionym.
Lapeirousia viridis (Ait) L. Bol. in S. Afr. Gard. 22: 276 (1932).

2. The circumscription of several genera in the *Gladiolineae* has been altered. The following name changes are made :

Gladiolus buckerveldii (L. Bol.) Goldblatt comb. nov.
Antholyza buckerveldii L. Bol. in Ann. Bol. Herb. 4: 118 (1927) basionym.
Petamenes buckerveldii (L. Bol.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932)

Homoglossum abbreviatum (Andr.) Goldblatt comb. nov.
Gladiolus abbreviatus Andr., Bot. Rep.: t. 166 (1801) basionym.
Petamenes abbreviatus (Andr.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932)

Anomalesia saccata (Klatt) Goldblatt comb. nov.
Kentrosiphon saccatus (Klatt) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932)
Anisanthus saccatus Klatt in Linnaea 35: 300 (1868) basionym.

In spite of the large number of described species of *Kentrosiphon*, the author recognises only one, but supports the variety proposed by Obermeyer (1961).

Oenostachys zambeziacus (Bak.) Goldblatt comb. nov.
Antholyza zambeziacus Bak. Handbk. Irid.: 232 (1802)
Petamenes zambeziacus (Bak.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 277 (1932)

Oenostachys huillensis (Welw. ex Bak.) Goldblatt comb. nov.
Antholyza huillensis Welw. ex Bak. in Tr. Lin. Soc. Bot. ser. 2, 1: 270 (1880), basionym.
Petamenes huillensis (Welw. ex Bak.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932).

Oenostachys vaginifer (Milne-Redhead) Goldblatt comb. nov.
Petamenes vaginifer Milne-Redhead in Hook. Ic.: t. 3478 (1951), basionym.

Several other species at present referred to *Petamenes* should also be transferred to *Oenostachys*, but without a knowledge of these and in the absence of material the author prefers not to do so for fear of adding unnecessary synonyms to the literature. For the same reason no species of *Acidanthera* has been transferred to *Gladiolus*.

3. *Curtonus* has been shown to be closely allied to *Crocosmia* and is incorporated in that genus:
   Crocosmia paniculata (Klatt) Goldblatt comb. nov.
   Antholyza paniculata Klatt in Linnaea 35: 379 (1868) basionym.
   Curtonus paniculatus (Klatt) N.E. Br. in Tr. Roy, Soc. S. Afr. 20: 270 (1932)
4. The genus *Anaclanthe* is incorporated in *Antholyza.* The following treatment is necessary:
   Antholyza plicata L.f. Suppl.: 96 (1781)
   Anaclanthe plicata (L.f.) N.E. Br. in Tr. Roy, Soc. S. Afr. 20: 269 (1932).

   Antholyza namaquensis (N.E. Br.) Goldblatt comb. nov.
   Anaclanthe namaquensis N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 269 (1932) basionym.

6. THE SIGNIFICANCE OF CYTOLOGICAL DATA IN THE IRIDACEAE

General discussion on the cytology of the Iridaceae and the significance of some cytological features.

6.1 POLYPLOIDY

It has been estimated by Stebbins (1950) that the proportion of polyploid species in the Angiosperms may be about 35%, but this figure is perhaps rather conservative judging by the data quoted by Reese (1957). In view of this, the number of polyploid species in the southern African Iridaceae is surprisingly low, for of the approximately 300 species which have been cytologically examined, only some 20 are polyploid. Of these, only 13 occur in the south-western Cape Province where the concentration of species is greatest, and where almost 250 of the studied species occur (Table 18, 19).

The distribution of polyploidy in different families and geographical areas varies considerably. In general, it has been observed to increase with latitude in the northern hemisphere (Reese 1957) though Stebbins has pointed out that changes in the composition of the flora usually accompany increase in latitude and that families where polyploidy is more frequent often become more common. The correlation between increased latitude and polyploidy does, however, still appear correct but to a smaller extent than previously suggested, when floral composition is taken into account.

A similar correlation between latitude and polyploidy was observed by Manton (1952) in the fern flora of Madeira and Britain, where polyploidy increases from 42% to 53%. Subsequently, she found the frequency of polyploidy to be 60% in the ferns of Ceylon (Manton 1953). This appears to indicate that it may not be latitude and the accompanying cold conditions that are the critical factor. Manton proposed that the observation could be explained on the basis of the disturbance of flora. Ceylon, which has a stratified flora, has a high rainfall and is subject to flood and landslide which disturb normal habitats and enable species not usually sympatric to grow near one another and hybridise. The suggested disturbance factor in the northern hemisphere is the extreme prehistoric glaciation which probably had a more marked effect on the environment than landslide and flood.

An increase in altitude would be expected to have a similar effect and this has been observed by Morton (1964), who showed that a representative sample of the flora of West Africa had 26% polyploidy while the tropical African mountains, Kilimanjaro and Mt. Cameroon had 47% polyploidy (compared to 38% in the northern Sahara and 70% in Greenland). The mountain regions have been partly glaciated at times and Morton suggested that environmental instability was the factor favouring increased polyploidy. Even when it is realised that the floral composition varies in the above areas, the correlation seems relevant.

The occurrence of polyploidy is known to vary greatly in different families. According to Stebbins (1956) it is particularly high in the Gramineae (70%) and also in the Cyperaceae, Rosaceae and Iridaceae amongst others, but absent from families such as the Curcurbitaceae, Fagaceae, Moraceae. It occurs commonly in some genera in a family and not others e.g. in the Salicaceae it occurs in *Salix* but not in *Populus*. In general it is most common in perennial herbs, less frequent in annuals and rare in woody plants. Stebbins' view that polyploidy is common in the Iridaceae can, in the light of the present study, be seen as incorrect but his information must have been based on northern hemisphere genera like *Iris* and *Crocus* where it is common.

An analysis of polyploidy in the Iridaceae shows similar inconsistencies in its distribution. Polyploidy is almost absent from the southern African members of the tribe *Sisyrinchieae*. *Aristea ecklonii* is one species which must be accepted as consistently polyploid, but in *A. glauca*, where a polyploid population was discovered, the polyploidy does not seem to be significant and is possibly a case of isolated autoploidy. *A. ecklonii* is a summer rainfall species, occurring along the eastern mountains of southern Africa.

Sisyrinchium, a New World genus, which occurs from Uruguay to Greenland, exhibits a high degree of polyploidy. This increases in both frequency and level in different species with an increase in altitude and latitude (Böcher, 1966). In contrast, no polyploid species have been found in *Bobartia*, believed to be a close ally of *Sisyrinchium*, and which occurs only in South Africa.

Polyploidy is also relatively uncommon in the southern African representatives of the Irideae and is absent from some genera. The highest frequency was observed in *Ferraria* and *Gynandriris* where one of the three species studied in each genus was polyploid. The polyploid species of *Gynandriris* is, however, unusual in its distribution, being the only member of the genus recorded for the northern hemisphere. In some of the other genera approximately a quarter of the species studied are polyploid, though in *Moraea* less than a tenth of those examined proved to be polyploid, and no polyploid species have been found in *Hexaglottis.*

Iris, which is widespread in the northern hemisphere and closely related to *Moraea*, is by contrast cytologically complex. It is clear that many species of *Iris* have a polyploid origin while others have evolved by aneuploidy from them. If these are also considered as polyploid, then the frequency is above 50% in this genus as a whole, though according to Simonet (1934) polyploidy is apparently absent in some sections of the genus.

It seems clear that in these two tribes, the *Sisyrinchieae* and *Irideae*, the potential for polyploidy is present but occurs only under certain conditions, the most obvious of which are increases in frequency with latitude in the northern hemisphere and to a lesser extent with altitude. This correlation is clearly in accord with previously accepted views and in *Iris* particularly, glaciation has been proposed to explain the phenomenon.

In the third tribe, the *Ixieae*, polyploidy is very uncommon. This tribe is predominantly African in occurrence though three genera are found in Europe and Asia. The majority of genera, however, occur exclusively in the south-western Cape Province and it is here, where polyploidy is most rare, that the majority of species occur. The observation in the other tribes, that the number of polyploid species is greater in the northern hemisphere is also noted for the *Ixieae*. All the species of *Gladiolus* occurring in Europe and Asia are high polyploids, while lower polyploids occur in the central African mountains and no polyploids at all are recorded from the south-western Cape Province. *Crocus* a fairly large genus, exhibits the greatest degree of polyploidy in the *Ixieae*, and it is almost exclusively European and Asian in distribution. As in *Iris*, several species have a polyploid origin, while others seem to have originated by aneuploid changes. The frequency of polyploid species has been established to be higher than 50% by some workers.

A possible explanation for the scarcity of polyploid species in the *Ixieae* in southern Africa and in the western Cape Province particularly, can be offered. Firstly the species do not appear to have one of the major requirements for polyploid speciation, hybrid infertility. It is well known (see section on inter-generic hybridisation) that interspecific hybrids can be obtained with ease in many of the genera, and that the hybrids are fertile so that genetic segregation occurs in the following generations. Secondly, the majority of species are endemics, particularly in the south western Cape Province where many of the species in the *Ixieae* are very localised.

It is suggested that much of the speciation in this group is fairly recent and that this has occurred almost entirely at the diploid level. If this is correct, then most species are fairly young and may not yet have developed internal barriers to reproduction which would cause hybrid sterility. It must be pointed out, however, that even in *Gladiolus* where polyploid species do occur, a degree of hybrid sterility is not a common phenomenon and most species appear to be interfertile.

In the *Ixieae* a single species each, of *Tritonia* and *Ixia*, were found to be polyploid and in both cases they were summer rainfall species. Two of the three polyploid species of *Romulea* found by de Vos (1965) in South Africa and the

TABLE 18

The frequency of polyploid species in the African genera of the Iridaceae, with comparisons to the non-African genera *Iris*, *Crocus* and *Sisyrinchium*. The approximate total number of species in the genus, the number that have been cytologically studied and the number of polyploid species in toto and in winter rainfall areas are given.

GENUS	Total No. Species	No. cyt. examined	No. polypld. species	No. polypld. species in winter rainfall area.
(SISYRINCHIEAE)				
Aristea	50	11	1	0
Nivenia	8	3	0	0
Klattia	1	1	0	0
Witsenia	1	1	0	0
Bobartia	12	3	0	0
Sisyrinchium	75	25	20	—
(IRIDEAE)				
Moraea	60	27	2	1
Dietes	6	4	1	0
Homeria	30	12	3	2
Galaxia	5	4	1	1
Gyandriris	10	3	1	0
Hexaglottis	4	2	0	0
Ferraria	10	3	1	1
Iris	200	(Not known exactly; estimated more than 50% polyploid.)		
(IXIEAE)				
Gladiolus	150	46	8	0
Romulea	90	±32	3	1
Geissorhiza	48	11	3	3
Tritonia	40	10	1	0
Ixia	44	14	1	0
Watsonia	70	20	1	1
Pillansia	1	1	1	1
Other African genera	±300	±100	0	0
Crocus	60	(Not known; estimated that 50% of species are polyploid)		

few African species of *Gladiolus* that are polyploid also occur in the summer rainfall area. As can be seen from Table 19, the frequency of polyploid species in the summer rainfall area is about 30%.

Only six species of *Ixieae* in the winter rainfall area were found to be polyploid, three of which belong to the genus *Geissorhiza*, one to *Watsonia* and one to *Pillansia*, suggested to be a relict polyploid. To this number, one species of *Romulea* can be added as judged from the chromosome numbers given by de Vos (1965) for that genus. This represents a frequency of about 3%. The correlation of increasing latitude or cold conditions does not seem to explain these striking differences between the southern African summer and winter rainfall species. The suggestion of Manton that the common factor is violent ecological disturbance is equally unsatisfactory for as a group, the species from both areas have similar ecological requirements. They usually grow in cooler areas, often on mountain slopes or plateaux. Both areas have a high rainfall, not noticeably different, nor is either of the areas known to be more geologically unstable or prone to landslides. Yet it remains clear that the frequency of polyploid species is far higher in all tribes in the summer rainfall area and this requires further investigation. The genus *Geissorhiza* seems to be an exception for three of the eleven species proved to be polyploid. The genus occurs only in the winter rainfall area. The reason for the relatively high incidence of polyploidy here also requires investigation.

TABLE 19

The frequency of polyploidy of the southern African representatives of the tribes *Ixieae* and *Irideae*. The number of species cytologically investigated, the number of polyploid species and the percentage of polyploid species is given and the tribes are divided into species occurring in either summer (s.rf.) or winter (w.rf.) regions.

TRIBE	No. species studied	No. polyploid	Approximate %
Ixieae w.rf. . . .	200	6	3%
s.rf. . . .	38	12	30%
Irideae w.rf. . . .	38	5	12%
s.rf. . . .	17	4	25%

It is not known whether the low frequency of polyploid species in the Iridaceae also occurs in other groups in southern Africa. Comparable cytological studies are few and not representative of the whole area. The Proteaceae are one family where the cytology has been fairly well studied and no polyploid species have been recorded in southern Africa. Norlindh (1963) found only two polyploids among the southern African species belonging to the tribe *Calenduleae* (Compositae) that he examined and both were summer rainfall representatives.

Ornithogalum (Liliaceae) is perhaps more comparable to the Iridaceae, being a perennial geophytic genus which, though widespread in South Africa, is more common in the winter rainfall region. Here polyploidy is extremely rare and perhaps only two true polyploid species occur out of thirty that have been investigated (Pienaar 1963). In the case of *Ornithogalum* both polyploid species occur in the winter rainfall region.

More cytological studies on African plants are obviously required before comments can be made about polyploidy in this part of the world. Except for the Iridaceae, comparisons are not yet possible between African and non African plants and until such studies are made, it will not be possible to observe any general trends.

6.2 CHROMOSOME NUMBER

There is considerable variation in chromosome number at the diploid level in the Iridaceae. Most genera are characterised by a particular number but aneuploidy occurs in *Sisyrinchium*, *Iris*, *Moraea*, *Romulea* and *Crocus*.

Chromosome number is a useful taxonomic and phylogenetic tool where variation occurs and is particularly valuable for genera where aneuploidy is found. The significance of chromosome number *per se* is not clear. A difference in number is a reproductive barrier in closely related species or genera, as it usually results in meiotic abnormalities in hybrids leading to sterility.

The actual mechanism for changes in basic number are known and proved only for decreasing aneuploidy and this has been suggested to be far more common than increase in number. As Jones (1970) has pointed out, various authors have explained the decrease in number as of possible advantage in changed relationships of genes resulting in new adaptive complexes and in the general tightening of linkage relationships.

Whether there is in fact any significance in the chromosome number in the family, it would seem that ancestral polyploidy can be discounted, for as discussed under the section on chromosome size, the quantity of chromosome material is very similar in all the genera of the *Ixieae* (disregarding polyploid species). The same can be said for the genera of the Irideae though the quantity here is not quite constant. Chromosome number has also been suggested to be of significance in the production of more or less variable offspring, particularly in annuals (Stebbins 1950, 1957). Aspects such as these require investigation in the Iridaceae although chromosome number may be quite without such direct adaptive significance in the family.

The widely held view that a decrease in chromosome number is more common than an increase seems to be confirmed by the present studies in the Iridaceae, but although this has been more common, the opposite process does occur. In the *Irideae* and *Ixieae*, where generic relationships are often fairly clear, decreasing aneuploidy has occurred in *Moraea*, *Hexaglottis*, in the *Watsoniineae* and possibly in the origin of *Romulea* and of *Chasmanthe*. In *Romulea* itself, decreasing aneuploidy has been more common but there seems little doubt that some degree of increasing aneuploidy has also taken place. Stepwise increase in number also seems to have occurred in the origin of *Gladiolus*, in the evolution of the *Exohebineae* and possibly in the origin of the genus *Galaxia*.

6.3 CHROMOSOME SIZE

The general size of the chromosomes, considered by Stebbins (1950) as a major characteristic of the karyotype, differs considerably in the Iridaceae. Differences in general chromosome size are known in many groups of Angiosperms, though size is, under normal circumstances, constant in a species. Increase in chromosome size in temperate climates is often observed and in some cases also a degree of morphological specialisation (Stebbins 1950). This trend is, however, not general and several exceptions are known. In some genera such as *Lilium*, an adaptive significance has been suggested for the large chromosomes in a cold climate (Stebbins 1966). Nevertheless, as Davis and Heywood (1963) pointed out, generalisations should be avoided and each case should be treated on its merits.

In the Iridaceae there are two distinct series of chromosome sizes with the difference in total chromosome length considerable. This difference has been used by the present author as one of the criteria for the recognition of tribes in the family. The tribe *Sisyrinchieae*, a group with small to medium chromosomes is believed to be the most primitive group in the family. The chromosome size is similar in the *Ixieae* with the exception of *Crocus*. The *Irideae*, a group with large chromosomes, must be regarded as karyologically specialised if the Iridaceae are a natural group which presupposes common ancestry.

Total chromosome volume is a more comparable measure than length because it takes into account the variation in width of chromosomes. It is believed to be directly proportional to the quantity of DNA present in the nucleus (Sparrow & Miksche 1961). Chromosome volume in selected genera in each of the tribes is compared in Table 20. Here the volume has been calculated by assuming the chromosomes are cylindrical and using the formula $\pi r^2 h$ where r is the radius or half the width, and h the total length of the chromosomes. There is probably some degree of error in measurement, particularly in width which is of the order of between 0,5 and 1,0μ. The error here may be about 10%. The length has been calculated by determining the average of the length of several karyotypes. This measure of chromosome size, though possibly prone to a considerable degree of error, seems to the present author a more meaningful measure than length alone, as used for example by Rothfels *et al.* (1966) in their study of the chromosome cytology of *Anemone*.

These calculations show that in spite of considerable variation in chromosome number in the groups with small chromosomes, both *Aristea* and members of the *Ixieae* have a similar chromosome volume and presumably the same quantity of DNA. In the *Irideae* the chromosome volume is more variable with a range from 40 to 90 cubic μ. Some of the smaller differences here may be ascribed to error, for small differences in the width would affect the result considerably but it is clear that error alone cannot account for the very high figure obtained for several species of *Moraea* with a diploid number of 12, e.g. *M. spathulata.* The remainder of the genera, including species of *Moraea* with diploid numbers of 20, have a similar chromosome volume and probably form a single group.

The high figures obtained for several of the species of *Moraea* suggests polyploidy but this does not seem possible as these have the lowest diploid number encountered in the genus. A possible explanation is that the DNA is arranged in the chromosome in a less dense manner or that the chromosomes

TABLE 20

A comparison of chromosome size in some genera and species of the South African Iridaceae. The basic number, total chromosome length, width, radius squared and total volume of each selected genus or species is shown.

Tribe & genus or species	Somatic Number	Total Chro. Length. μ	Chro. Width. μ	Radius^2 (to three decimal places)	Volume πr^2h μ^3
SISYRINCHIEAE					
Aristea	32	40	0,5	0,063	7,8
Bobartia	20	80	0,6	0,09	22,6
IXIEAE					
Tritonia	22	40	0,5	0,063	7,9
Babiana	14	38	0,5	0,063	7,5
Therianthus . . .	20	40	0,5	0,063	7,9
Watsonia . . .	18	40	0,5	0,063	7,9
Ixia	20	38	0,5	0,063	7,5
Sparaxis	20	36	0,5	0,063	7,0
Hesperantha . .	26	40	0,5	0,063	7,9
Gladiolus . . .	30	36	0,5	0,063	7,0
IRIDEAE					
Dietes	20	100	0,75	0,14	45
Moraea spathulata (2n=12) . . .	12	100	1,1	0,3	95
M. ramosissima (2n=20) . . .	20	110	0,75	0,14	50
M. ciliata (2n=20) . . .	20	70	0,9	0,2	44
Homeria . . .	12	84	0,9	0,2	53
Galaxia	16	80	0,8	0,16	40
Hexaglottis . . .	12	75	0,9	0,2	47

are polynemic (i.e. multistranded). This same explanation can be offered for the great difference in chromosome volume between the *Ixieae* and *Irideae* where the differences are of the order of six times and suggests a fundamental difference between these groups. Several attempts were made to ascertain whether the difference in size could be attributed to multistrandedness of chromosomes. This condition was sometimes observed in species with large chromosomes but the small chromosomes were themselves too small to observe the condition even if it did occur.

The exceptional genus in the *Ixieae* is *Crocus*, which grows actively under very cold winter conditions. The same cannot be said for the majority of the *Irideae*. Certain species of *Iris* grow in a similar environment to *Crocus*, but none of the other genera of the *Irideae* studied here do, and the large chromosome size cannot be ascribed to the supposed adaptation to cold conditions. *Morea* and *Homeria* grow under the same ecological conditions as the *Ixieae* and appear even to fill similar ecological niches. The difference here is perhaps an ancestral condition that has persisted rather than an adaptive one.

The significance of differences in size of chromosomes remains unclear and there are probably several different explanations in various groups of plants. Multistrandedness and perhaps lateral replication of chromatids are also suggested to occur in some plants, but here the significance is not explained. Further investigation seems fundamental to the understanding of chromosome structure and the genetic and taxonomic significance of size differences remain for the most part unknown.

7. GEOGRAPHICAL DISTRIBUTION

The geographical distribution of the family in relation to cytology and possible phylogeny

Sisyrinchieae

Genera in this tribe are spread throughout the world, but the majority are found in the southern hemisphere. There are three centres of distribution, southern Africa, Australia and South America. The genera occurring north of the equator are *Sisyrinchium* and *Belamcanda*, the latter specialised. In *Sisyrinchium* only polyploid species occur in the northern hemisphere while the South American representatives are diploid or low polyploids.

This tribe, the least specialised in the Iridaceae is apparently of southern origin. It shares with a large number of other groups, e.g. Proteaceae, Restionaceae, this peculiar southern distribution which has been regarded as evidence that the southern continents were at some time in the past part of a single land mass known as Gondwanaland. This evidence of present and past floral similarity on the southern continents is regarded as evidence for the theory of continental drift, which though much ridiculed by geologists in the past, is now gaining acceptance.

Irideae

This tribe is mainly Central and South American and African but is well represented in Europe and Asia by *Iris* and in Australasia by one species of *Dietes*. Except for *Iris*, and *Tigridia*, the majority of species occurring north of the equator belong to southern genera. *Iris*, which is a somewhat specialised genus, is believed to be derived from the southern genus *Dietes*. Thus this tribe, predominantly southern in distribution, probably also has its origin in the areas believed to have been part of Gondwanaland.

Ixieae

Except for the specialised *Crocus*, the tribe is African in distribution and most of the genera have an exclusively southern range. The cytology and classification are fairly well known and it appears that many of the subtribes have a central African origin.

The distribution of the genera and subtribes has been discussed individually in an earlier section. Of the ten subtribes recognised by the present author, eight are sufficiently well understood to be commented on. In the subtribes *Ixiineae*, *Tritoniinieae* and *Hesperanthineae*, the most primitive genera are distributed irregularly in southern and tropical Africa, being confined to mountain ranges, e.g. *Hesperantha*, *Dierama*. The *Gladiolineae* and *Crocineae* are both believed to be specialised from the *Hesperanthineae* and their most primitive genera occur in the Cape Province. These are believed to have originated in the south western Cape Province and have spread into Africa and Europe where *Romulea* and *Gladiolus* are found. *Crocus*, the predominantly Mediterranean genus believed to be derived from *Romulea* appears to have originated in the eastern Mediterranean region. As already discussed, a reverse origin seems unlikely for the most primitive species in these genera are found in the Cape Province and the European species of *Gladiolus* and *Romulea* are high polyploids.

The *Babianineae* and *Watsonineae* also appear to be southern in origin, for the least specialised species occur in the south western Cape Province. Individual species of *Babiana* occur in Rhodesia and Socotra but in both cases the species are specialised. *Watsonia* also occurs outside the Cape Province, in the eastern mountains as far as the northern Transvaal and in Madagascar, but again these species are more specialised than some found in the Cape Province. The *Exohebineae* are a poorly understood group but also seem to have their origin in the south western Cape Province for it is here that the least specialised species, *Tritoniopsis leslei* occurs.

It appears that the *Ixieae* arose in Africa. Whether Cape or tropical African in origin is not clear for subtribes have clearly originated in both areas. It is suggested that the tribe is primarily Central African in origin though poorly represented there today. With changes in climate and topography over millions of years, the tribe has become confined to tropical African mountain zones or has found refuge in the winter rainfall region of the Cape Province. Here great speciation has occurred which is believed of fairly recent origin. The most specialised tribes appear to have evolved here and some genera have spread from the Cape through Africa to Europe.

8. SUMMARY

The karyotypes of the southern African members of the *Iridaceae* are described and discussed with regard to taxonomy, phylogeny and evolution of the family. The karyotypes of 225 species in 43 genera were investigated, 186 of these being new cytological records.

Hybridisation is discussed in the family with special reference to intergeneric hybrids. Nineteen intergeneric crosses were attempted and five were successful. The significance of the intergeneric crosses is then discussed in relation to the taxonomy of particular genera.

The different systems of classification of the Iridaceae are evaluated, those of Bentham & Hooker, Pax, Hutchinson and Lewis being regarded as the most significant. The cytological evidence is then discussed in relation to the major subdivisions of the family. It was observed that the chromosomes fell into two distinct size groups, small and very large, which were found to correspond to the tribes proposed by Bentham & Hooker, the genera with large chromosomes belonging to the *Irideae* and those with small chromosomes to the *Sisyrinchieae* and *Ixieae* respectively. The genus *Galaxia* with large chromosomes is shown to be incorrectly placed in the *Sisyrinchieae* and Lewis' contention that this genus be placed in the *Irideae* is supported.

The cytological data are discussed at generic level, each tribe being dealt with separately. In general, it was observed that a genus or group of genera have a distinctive karyotype and that this could be linked with certain morphological features. In this way it became possible to determine intergeneric relationships and to recognise subtribes in many cases.

In the *Sisyrinchieae*, *Aristea* with a basic number of 16 is shown to be allied to the woody genera, *Nivenia*, *Klattia* and *Witsenia* also with a basic number of 16. Evidence strongly suggests that these form a single subtribe and should not be placed in different tribes as suggested by Weimarck and by Lewis. *Bobartia* was found to have a basic number of 10 and to have somewhat larger chromosomes than *Aristea*. It is shown to be a natural group itself, but is believed to be only distantly related to *Aristea* and its allies and a separate subtribe is proposed for this group.

In the second tribe, the *Irideae*, *Dietes* is shown to have a basic number of 10 and one species, *D. bicolor* is suggested to be a tetraploid. *Dietes* is suggested as the ancestor of both *Iris* and the genus *Moraea* and is shown to be intermediate between these two genera so that it cannot correctly be included in either. An ancestral basic number of 10 is suggested for *Iris* and for *Moraea*.

A large number of species of *Moraea* were studied and this genus was found to be heteroploid with haploid numbers of 10, 9 and 6. *M. ramosissima* with a basic number of 10 is suggested as the ancestral type of the genus and is linked to *Dietes*, which has a similar karyotype. The classification of *Moraea* into sections and subgenera by Baker is reviewed and is in general confirmed, though a few species were found to be misplaced.

Two representatives of the genus *Gynandriris* were studied and found to have a karyotype like that of the previously studied European species which is shown to be polyploid. The karyotype of the genus is found to be very similar to that of some species of *Moraea*. The treatment of Lawrence in placing the European species of *Gynandriris* in *Iris* is shown to be inconsistent with the maintenance of *Gynandriris* and *Moraea* in South Africa, genera to which the European species of *Gynandriris* is clearly more closely allied.

Several representatives of the genus *Homeria* were studied and the basic number was found to be 6. One species *H. breyniana* was found to be tetraploid and a variety of this species (var. *aurantiaca*) to be hexaploid. The similarities between *Homeria* and *Moraea* are discussed and shown to be rather poorly defined but it was concluded that *Homeria* must be maintained if only for convenience.

The genus *Galaxia*, with a basic number of 8, and large chromosomes is shown conclusively to belong to the *Irideae*. Its suggested allies are *Homeria* or *Moraea*. One species, referred to *G. ovata*, was found to be polyploid. *Hexaglottis* was also found to have large chromosomes. One species had a basic number of 6 and the other 5. The latter species, *H. virgata* is suggested to be specialised and to have been derived by aneuploid reduction.

The genus *Ferraria* was found to have a basic number of 10. One species, *F. undulata*, is shown to be consistently hexaploid while the other two that were studied were diploid. It is suggested that *Ferraria* is a specialised offshoot of *Dietes* and not to be allied to the American genus *Tigridia*, which has a different karyotype and morphology.

It is proposed to recognise three subtribes in the South African *Irideae*, one the *Iridineae* being widespread and including *Iris*, *Moraea*, *Dietes* and *Gynandriris*. The *Homeriineae* comprising *Homeria*, *Galaxia* and *Hexaglottis* and the *Ferrariineae* comprising only *Ferraria*, are exclusively southern African in distribution.

The genera in the tribe *Ixieae*, which is characterised by rather small chromosomes can be conveniently divided into ten groups which are designated as subtribes. The cytological data show that Hutchinson's classification of the genera in this group into three tribes based on floral morphology, is incorrect as genera with similar karyotypes and vegetative features are often placed in different tribes in his system. Lewis' classification of this group is found to compare very well with the cytological data though it was found convenient to subdivide one of her proposed subtribes, the *Ixiineae*, into four distinct subtribes. Another of her subtribes, the *Watsoniineae*, is divided into three subtribes which are suggested to be rather distantly related to one another.

In general it is found that the cytological evidence can best be correlated with vegetative features and that the nature of the corm, leaves, bracts and to a lesser extent the nature of the stigma branches, are the most significant features in this respect.

In the first of the subtribes, the *Watsoniineae*, only four genera are recognised including *Pillansia* which Lewis regarded as belonging to a separate subtribe This genus is found to be consistently polyploid and is suggested to be a relict tetraploid. A decreasing aneuploid series is suggested in this tribe leading from *Pillansia* (basic number 11) to *Watsonia* (basic number 9). *Watsonia bulbillifera* is found to be a sterile triploid, reproducing by cormlets alone. A possible ancestry is suggested for this species.

The second subtribe, the *Lapeirousiineae*, comprises only a single genus, *Lapeirousia*. Only two of the recognised subgenera, *Ovieda* and *Sophronia* are admitted to the genus and the third, *Anomatheca* is recognised as a valid genus, allied to the genus *Freesia*. Cytological and morphological evidence is cited to substantiate the differences between *Lapeirousia* proper on the one hand and *Anomatheca* and *Freesia* on the other. One species, previously referred to *Lapeirousia*, *A. fistulosa*, is shown to belong to *Anomatheca*. The tribe *Freesiineae* is proposed for *Anomatheca* and *Freesia*.

The four genera *Geissorhiza*, *Hesperantha*, *Schizostylis* and *Engysiphon* are found to be a natural group, sharing a basic number of 13 and several similar morphological features. *Melasphaerula* with a basic number of 11 is placed with these genera because of several morphological similarities. The subtribe *Hesperanthineae* is proposed for this group. The genus *Geissorhiza* is unusual in that three of the eleven species examined are found to be polyploid.

Lewis' interpretation of the subtribe *Crocineae* Bentham & Hooker (*Romulineae* of Lewis) is supported and it is shown that the three genera in this group are all heteroploid. The position of *Crocus* in this subtribe is questioned as it is the only genus in the *Ixieae* with very large chromosomes, although morphologically it seems to be correctly placed here. The possible origin of *Romulea* is discussed and *Geissorhiza* is suggested as a likely ancestor. Following this suggestion, a basic number of 24 for the genus and subtribe is proposed.

Gladiolus and its suggested allies were studied and all are found to have a basic number of 15. The existence of a polyploid series in the species in the summer rainfall region of Africa and the Mediterranean region is confirmed and on this basis a southern origin of the genus is proposed. All the species in the winter rainfall region of South Africa that have been studied are diploid, and those that are least modified occur here. The suggested origin of *Gladiolus* from *Geissorhiza* is discussed and if correct must have been accompanied by increasing aneuploidy. The occurrence of different levels of polyploidy in some species is mentioned, in particular *Gladiolus natalensis*, where triploid, tetraploid and pentaploid individuals were found in a single population.

The cytological evidence confirms the close relationship of *Acidanthera*, *Radinosiphon*, *Homoglossum*, *Petamenes* and *Anomalesia*, while the morphology of *Oenostachys* and *Kentrosiphon* indicates that these are also allied to this group. Intergeneric hybrids between several of these and *Gladiolus* have been previously recorded or were produced by the author, which confirms the close relationship of these genera. Several changes in circumscription of genera were proposed.

The subtribe *Ixiineae* proposed by Lewis is reduced to comprise only four genera, *Dierama*, *Ixia*, *Sparaxis* and *Synnotia*, all of which share a very similar karyotype. The status of *Synnotia* is critically discussed and it is concluded that it could be included in *Sparaxis* though this step may not be convenient. The possible evolution of this group is outlined.

The new subtribe, *Tritoniineae* is proposed for *Tritonia* and its allies, cytological similarities again pointing to the relationship. The genus *Curtonus* is treated as a species of *Crocosmia*. *Chasmanthe* is placed in this group although it has a slightly different karyotype. Lewis' subtribe *Babianineae* is supported on cytological grounds but *Anaclanthe* is included in *Antholyza* leaving only two genera in this subtribe. The proposed subtribe *Exohebineae* of Lewis is also supported. The two genera in this group have the highest chromosome numbers in the family, barring polyploid species.

The cytology of the family was then discussed in general. Polyploidy, previously believed common in the family, is shown to be rare, especially in the winter rainfall area of the Cape Province. Possible reasons for this are discussed. Chromosome number and size are briefly discussed and the often observed higher frequency of the decreasing aneuploidy is confirmed.

A brief discussion of the geographical distribution of the family led to the suggestion that the family originated in the southern hemisphere, possibly in prehistoric Gondwanaland. The *Ixieae* are suggested to be African in origin with a few representatives in Europe and Asia. The possible origin of some subtribes in the *Ixieae* is outlined.

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